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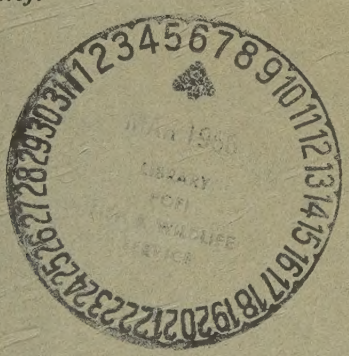
Production and a Pelagic Fishery

By D. H. CUSHING
Fisheries Laboratory, Lowestoft



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Preface

In every ocean there are large stocks of pelagic species of fish that are only exploited at their fringes. For example, on the European side of the Atlantic, pilchards, or closely related species, extend from the English Channel to the Cape of Good Hope, and are fished only at a few points in their distribution. Mackerels, tunas, and members of the Carangidae, are, similarly, fished mainly at the margins of their distribution.* Unknown factors govern the aggregation of the shoals of these species, in areas where they can be caught conveniently.

Among such fisheries there has been from time immemorial one for herring in the summer in the northern North Sea. Work of previous authors has made it reasonably certain that the major interest of the fish is in feeding on the common copepod *Calanus finmarchicus* Gunner. In this fishery there seems a fair possibility of reaching an understanding of those factors that govern success or failure. The present paper attempts the first steps towards achievement of that understanding.

*UNSCCUR papers, Vol. VII. Chart p. 61.

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Part I

Introduction: The *Calanus*-herring Relation

rmen and fishery naturalists have known for a long time that in temperate waters pelagic fish n the early summer. As the food occurs in large patches, it is likely that the fish will be l near them. For example, it can readily be shown that herring aggregate on to patches of *us*. The condition of aggregation of the fish on to their food patches can best be described ms of numbers of fish and food within one water mass. Using the relation between food and roduction in *Calanus* established by Marshall and Orr (1952), it is probable that the recruitment ung stages of *Calanus* into the aggregation system depends upon the plant production. At ther end of the system, it can be shown that the searching behaviour of the drifter fleet in time pace depends to a certain extent upon the distribution of the fish, and consequently the numbers h available are related to this behaviour of the fleet. These are all factors necessary to the rstanding of the *Calanus*-herring relation.

describe the system from the plant production to the searching behaviour of the drifters is short step from a full study of production. In this paper, production will not be approached the point of view of comparing water masses between regions and seasons, but from the point ew of understanding the vagaries of a feeding fishery. This introduces the concept of useful uction, which is that fraction of production which contributes to the yield of pelagic food s within a year. This has its effect on the yield of pelagic food fishes in two ways:

the increment of fish flesh per year due to growth (not recruitment) depends upon the production of fish food during that year;

the availability of the pelagic fish, in temperate seas, for catching depends partly upon the duration of the feeding systems in the early summer.

e factors affect the mean weight of each fish landed in the year and the mean catch of pelagic anded during the season of the feeding fishery.

ook (1886) was the first to draw attention to the relation between *Calanus* and herring and ords are still the most adequate statement of the situation: " Loch Fyne herring feed ravenously ie immense shoals of copepods which make their appearance in May. The commonest form *lanus finmarchicus*, a species which is almost the sole food of the herring in Loch Fyne." In Professor Hardy published his important work on the food of the herring; his Appendix B s that the herring caught in the spring fishery off Lowestoft (March and April) fed predominon *Ammodytes*. Off Shields, however, the Appendix shows that *Calanus* was much the most rtant food in May and June. Savage (1937) extended this work, and for five years in the ier *Calanus* was of the greatest importance in numbers (but not always in volume). This usion was supported by Jespersen (1928 and 1936) in the North Sea and off Iceland (1932), y Boldovsky (1941) in the Arctic. No other animal consistently makes up a greater proportion lume of the herring's food at this season. It is possible that *Calanus* is small enough to occur ite dense patches; and perhaps *Calanus* is large enough to make an individual fish stop to it; in this way an aggregation of fish would take place on the *Calanus* patch.

e time of year at which *Calanus* predominates in the plankton can be found by examination ankton samples and herring guts. Savage (1926) had found in July that there is a greater ortion of *Calanus* in the guts than in the plankton; for *Temora*, however, the proportions were the same. Jespersen (1928) showed that the proportion in gut and plankton were comle for *Calanus*, *Temora*, *Paracalanus* and *Pseudocalanus*. Brook and Calderwood (1886) nstrated that *Calanus* is the main food of the herring in May and June off the east and west of Scotland. In 1906, Scott wrote that the greatest quantity of *Calanus* in herring guts red in April off Shetland, in May and June off Stornoway, and in April in Loch Fyne and in lyde. In the southern North Sea, Savage (1937) found the greatest volume of *Calanus* in the g guts in May; Ogilvie (1934) confirmed this observation for the northern North Sea. In

the eastern North Sea Jespersen (1936) demonstrated that the herring feed most intensive *Calanus* in May and June. This is also true of the Clyde (Marshall, Nicholls and Orr, 193 is interesting to notice that the related species *Clupea pallasii* contained 98 per cent *Calanus* off British Columbia in April and May (Wailes, 1936). To sum up, the time of abundan *Calanus* in herring guts is in the early summer.

It would indeed be surprising if a corresponding time of abundance of *Calanus* in the sea di emerge from plankton studies. Damas and Koefoed (1907) were the first to demonstrate it, i.e. *Calanus* is the commonest copepod in the Greenland and Norwegian Seas in May; this was firmed by Ruud in 1929. In the " Plankton of the Offshore Waters of the Gulf of Maine ", Bi (1926) showed that *Calanus* comprised 80 per cent of the copepods and that there was a pe numbers in May, after which the *Calanus* populations declined. Farran (1928) showed tha greatest numbers of *Calanus* were found off S.W. Ireland in May; Bogorov (1934) demonst the same pattern off Plymouth, as did Marshall, Nicholls and Orr (1934) in the Clyde. Gil (1936) found the greatest quantity of *Calanus* in Scottish waters between April and May

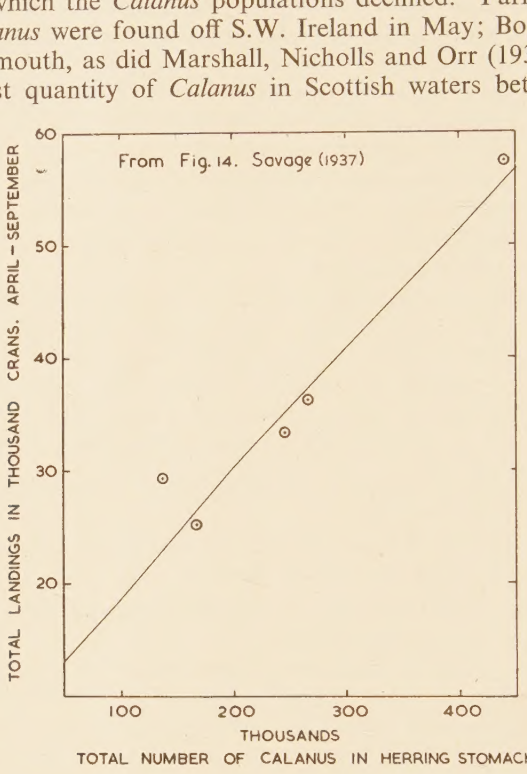


FIG. 1. LANDINGS OF HERRING AND NUMBERS OF *Calanus* IN HERRING STOMACHS
The landings are total landings at North Shields for a whole season, in thousands of crans and the numbe of *Calanus* are in thousands. Each point represents one year's observations.

Wimpenny (1937) caught the highest numbers of *Calanus* on the Flamborough Line in Ma the Bay of Fundy and in the Gulf of Maine the peak of *Calanus* numbers was found by Fish in May; this observation was confirmed in 1937 by Clarke and Zinn. Using the plankton rec Rees (1949) has shown that the largest numbers of *Calanus* are found in the western Nort in May and June.

Thus the generalization can be made that herring feed most intensively on *Calanus finmar* in May and June. It is interesting that this is consistent for very wide areas of the northern

It has long been assumed at Lowestoft that the basis of the Shields fishery lies in the C patches offshore; this is the point of Savage's long series of observations published in 1937. *Calanus* can occur in large patches was first pointed out by Bigelow in 1922 when he descr patch 50 miles long off George's Bank. *Calanus* occurs at some little distance off Shields (Jorg 1924, Wimpenny 1933, Gibbons 1936, Hardy *et al.* 1936); a discrete patch centred about 40 off the port is shown in an unpublished figure of Savage's. It was this figure that led to the of the Shields area for a study of the consumption of *Calanus* by the herring.

The dependence of the fishery on the density or distribution of *Calanus* is not at first s very clear one. In 1906, Paulsen wrote of the dependence of the N. Icelandic herring fish

nus in June. Wimpenny (1933) demonstrated a relation between the presence of *Calanus* on Flamborough Line in August and the herring landings from the Flamborough area; it is not vn whether these fish were actually feeding on the *Calanus*. Professor Hardy and his colleagues 5) have published a large number of associations between " rich " *Calanus* and good landings, or " *Calanus* and light landings. In particular, Lucas (Hardy *et al.*, 1936) was concerned with Shields area and it is interesting that he found a positive association in May and June, but a tive one subsequently; this can well be explained on the assumption that the herring have all the *Calanus* during the first period, as indeed Dr. Lucas himself suggests. Hardy (1936) a very interesting relation between the numbers of *Calanus* on the indicator discs and the landings in the Scottish area, showing that rich *Calanus* was associated with high average ngs. A different phenomenon is shown by Savage (1937) when he related the quantity of *nus* in the stomachs which is greatest in May and June and the total landings *for the whole ner* for five years at Shields (Fig. 1). Now, Savage's Fig. 10 (1937) shows that, in general, the five years' work, the herring landings increase at the end of June or during July, i.e., when ng has been reduced. The magnitude of these later landings, which composed the bulk of the ry, seems to depend upon the intensity of feeding in the earlier period. Table IX in Savage's r gives quite a strong suggestion that high herring landings *for the whole summer* are related *early* and rich supply of *Calanus*. These facts may be summarized in the following way: the

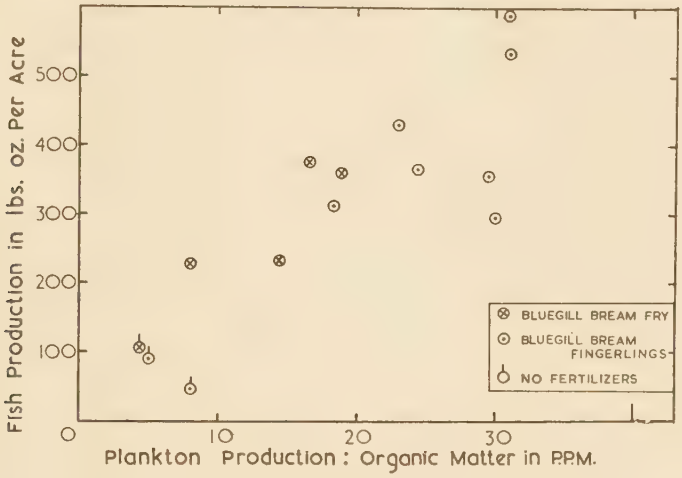


FIG. 2. PLANKTON PRODUCTION AND WEIGHT OF FISH
Observations from fertilized ponds, through one season (from Smith and Swingle, 1938).

nus populations are depleted and the intensity of feeding has been halved by the end of June age's Fig. 9), yet it is from this time that the landings increase.

e magnitude of drift net landings of herrings is likely to depend on the size of shoals: compare hields' landings (*c.* 5–10 crans per boat) where shoals are small, with the East Anglian land- (*c.* 30–50 crans per boat) where the shoals can be very large. It is possible that the shoals er to their minimum size before or during the first stages of feeding on *Calanus*. So long as is more than enough *Calanus*, searching within the patch will be at a minimum and shoals be small; as the *Calanus* thins out, searching within the patch, now broken into a series of er patches, will increase, and shoals, no longer dispersed by continuous feeding activity, might ncrease in size. Hence there might be a relation between the length of time between complete gation and complete annihilation, and the subsequent level of the landings. If this period is extended, there is then time for the shoals to thicken up as they " mop up " the *Calanus*. s is so, then Savage's Fig 14 (1937) makes a great deal of sense. It may well be that the level ndings in a feeding fishery is directly related to the time for destruction of the *Calanus* patch; of course, would be directly associated with the *Calanus* production.

e purpose of this paper is to try to derive the factors that may be used in a dynamic analysis nkton production and its effect on the aggregation of fish shoals.

e simplest demonstration of the relation of plankton production as a whole to fish production t given in Smith and Swingle (1939). Fourteen small ponds were stocked with counted numbers

of bluegill bream (fry and fingerlings) in May and they received four applications of inorga fertilizers. The ponds were drained in November and the final weight of fish was record Plankton production was also measured, as organic matter in p.p.m. each week and a mean plank production for each pond over the period was derived. The results are plotted in Fig. 2, show a clear but curvilinear relation between weight of fish and production of mean plankton. Th a clear and neat example of the dependence of fish production on plankton production, e considered as a whole.

Off the north-east coast of England, a grid of stations was laid down, extending seawards as as 130 miles. At each station, nutrient salts, phytoplankton and zooplankton were sampled the usual procedures; between stations, an estimate of pelagic fish was made by the use method of echo survey. This grid of stations was repeated on five successive cruises.

The results of these cruises lead, at this stage, to four new types of estimate:

(*a*) From patches identifiable through three cruises, are made estimates of the change in num in certain populations of plankton organisms.

(*b*) From the echo survey, an estimate is reached of the aggregation of pelagic fish on to pat of their food.

(*c*) From estimates of diatom division rates, quantities of plant food taken by each plan animal per day, are derived.

(*d*) From measurements of the phosphorus content of diatoms and from the estimated p production, an estimate of the rate of regeneration of phosphorus per day was made.

With these estimates, we would be able to find the dependences of the different levels of the sy upon each other. As we are dealing with numbers of plants produced, numbers of plants e numbers of animals eating, and numbers of fish aggregating, the whole system is described dynamic cycle. In order to understand the complex cycle in the open sea, it is necessary at to limit study only to the useful production which contributes to the feeding of the her " Useless " production processes (e.g., the production of jellyfish) are not considered in this p because it is unlikely that they have much effect on that part of the " useful " cycle that w elucidating. It will be shown that estimates derived from these five cruises provide an accou the cycle that promises full understanding by further research along the same lines.

Part II

he Estimation of Numbers and Distribution of *Calanus* Patches and Diatom Patches

1. Introduction

rder to estimate the changes in numbers of plants and animals in their patches in the sea, it is ssary to devote a good deal of attention to sampling and counting techniques, in which there many uncertainties.

2. μ-flagellates

STIMATES OF NUMBERS

timation of the numbers of μ-flagellates in the sea is at the moment difficult. Lohmann (1902;), by centifuging small quantities of sea water, estimated that the proportion of numbers of ms to numbers of μ-flagellates was 6:1 in Kiel Harbour and 7:1 in the North Atlantic. Using ame methods, Lillick (1938) found about the same ratio off the north-east coast of America. 1 (1919), employing a culture method, demonstrated that many species of autotrophic flagellates in the sea. Knight-Jones and Walne (1951), using this type of method, have given estimates e density in numbers of *Chromulina pusilla* Butcher in the sea. Cole and Knight-Jones (1949) introduced a method of concentrating sea water through a collodion membrane, using a Cole filter; they then count the μ-flagellates in the concentrate with a haemacytometer.

chniques for the estimation of numbers of μ-flagellates are in an early stage of development, hey were found to be sufficiently reliable to show that the gap in the food chain is not serious full estimation of numbers was omitted. Samples for dilution were collected in duplicate at stations only on each of Cruises VII, VIII and IX, Sir Lancelot, 1949. Samples of sea water taken at 10 m., 20 m. and 30 m. at night (to avoid the destructive effect of sunlight). These les were mixed in one bottle and dilution cultures were set up from this bottle in Erdschreiber: 0 ml. of Erdschreiber were added 10 ml. of sea water. There were 15 sterile tubes (each con- ng 30 ml. of Erdschreiber), to 5 of which were added 10 ml. of the sea water-Erdschreiber ure, to a further 5 of which were added 1 ml. each of the mixture, and to the last set of 5 were d 0·1 ml. each of the mixture. These cultures at three levels of dilution were then put in a nostatically controlled cabinet and brought home at sea temperature in artificial light.

e cultures were kept in a north window in the laboratory for about a month and were then ined. The number of tubes that contained μ-flagellates at each of the three dilutions was ded, and from Swaroop's (1938) tables the number/ml. in the sea and their probable errors estimated. These μ-flagellates were all very small, about 1—2μ in size.

. Cole's concentrator was used (Cole and Knight-Jones, 1949) on a cruise in the English nel in April 1950. The samples were concentrated fifty times by filtration, killed in Lugol lution of iodine in potassium iodide and distilled water, which had been tested satisfactorily fixative on cultures before going to sea) and counted in a Petrov-Hausser counter; this counter naemacytometer with a depth of 20 μ. This means that the field may be examined under a . oil immersion lens and the organisms identified as μ-flagellates. The most marked result he great difference between the dilution estimates and the Petrov-Hausser counter estimates. ification by the dilution method is certain, but it is possible that competition between the species of μ-flagellates might have had an adverse effect on the estimate of numbers; it is possible that the culture medium has a selective effect, being a better medium for some nisms.

experiment was set up to test this effect, the numbers of two monotypic cultures and one d culture were estimated after a culture period of three weeks, using the Petrov-Hausser counter

for a live count (without the concentrator as the cultures were dense) and using the dilution meth The results are shown in Table I. It seems likely that the anomalous result with *Hemise rufescens* is due to competition with the unnamed μ-flagellate.

Table I

Comparison of Petrov-Hausser counter and dilution culture; suffices indicate the number of replicate counts

	Petrov-Hausser counter	*Dilution culture*
Isochrysis galbana. Parke	465_{10}/mm.³	542± 330/ml.
Dicrateria inornata. Parke ..	115_{10}/mm.³	542± 330/ml.
Hemiselmis rufescens. Parke .. and an unnamed μ-flagellate	100_{10}/mm.³	6± 4/ml. (both species coun

Note: The densities in numbers given by the two methods are not completely comparable because 542± 330/ the maximum density expressed in Swaroop's tables; they are, however, comparable in the culture of *Hemis rufescens*.

Estimates of numbers of μ-flagellates by sedimentation (Aurich 1949), by dilution (Kn Jones, 1951; and my observations in 1949) and by use of the Cole concentrator and Petrov-Ha counter are set out in Table II.

Table II

Estimated numbers of μ-flagellates per ml.

Method	*Station*	*Number/ml.*	*Mean number/ml.*	*Author*
Sedimentation .. (Jod-Jodkali fixation)	Coastal, inner ,, outer Open sea	242, 150, 182, 68 146, 65, 140 4, 14	160 117 9	Aurich (194
Dilution culture ..	S. Bight Firth of Forth Off Flamborough Arctic Ocean Helford River	79 542 130 11 5,420	79 542 130 11 5,420	Knight-Jon (1951)
Dilution culture ..	Shields area Cr. VII, Sir Lancelot, '49 Cr. VIII, Sir Lancelot, '49 Cr. IX, Sir Lancelot, '49	 0·23 ± 0·11, 0·11 ± 0·06 0·14 ± 0·07, 0·21 ± 0·10 5·42 ± 3·30, 0·32 ± 0·17 0·24 ± 0·12, 2·78 ± 1·43 0 0 0 0	 $0·17_{(2)}$ $0·18_{(2)}$ $2·87_{(2)}$ $1·51_{(2)}$ 0 0	
Cole concentrator; Petrov-Hausser counter	English Channel Cr. VII, Sir Lancelot, '50 Sta. 39 Sta. 30	 250 2,600	 250 2,600 $583_{(8)}$	Mean n /ml. fro observat

(*Note:* Suffices indicate the number of observations contributing to the mean.)

It seems probable that the estimates using the Cole concentrator and the Petrov-Hausser co are the most reliable. Thus numbers of μ-flagellates may sometimes be high. Their impor as food for *Calanus*, however, would depend upon their biomass, for the calculation of whic number 583/ml. from Table II will be used.

STIMATES OF PLANT VOLUME

ıe first line of Table III gives the approximate volumes in μ^3 of the commoner diatoms on se VI, Sir Lancelot, '49. The principal simplification used was that chaetocerids were assumed e cylindrical and spineless. These volumes, which are derived from many measurements, multiplied by the mean numbers per litre of each diatom to give diatom biomasses by species in r litre. Included in the table is an estimate of the biomass of one μ-flagellate at this time (the me used was that of *Chromulina pusilla* and the number/ml. was taken from Table II). It will en that although the biomass of the μ-flagellates is by no means insignificant, it is a great deal han that of the diatoms. It is interesting that the middle sized diatoms (*Thalassiosira gravida* e, *Lauderia borealis* Gran and *Ditylum Brightwellii* (West) Grunow) comprise the greatest volume. In this context Harvey's observation (1937) that *Calanus* appears to select *Lauderia Ditylum* is most relevant.

Table III

Plant volume in μ^3 per litre for the commoner diatoms on Cruise VI, Sir L., '49

	Asterionella japonica. Cleve	*Chaetoceras compressus.* Lauder	*Thalassiosira gravida*	*Rhizoso lenia hebetata* Bailey (Granemend)	*Chaetoceras densus.* Cleve	*Lauderia borealis*	*Ditylum Bright-wellii*
ıe in μ^3 ..	821 (239)	1,584 (164)	11,768 (251)	13,403 (149)	18,407 (92)	49,232 (87)	156,002 (143)
ers/litre..	12,058 (42)	9,281 (42)	23,581 (42)	158 (42)	386 (42)	2,244 (42)	219 (42)
ıe × ers in μ^3	$9{\cdot}9 \times 10^6$	$14{\cdot}7 \times 10^6$	$277{\cdot}5 \times 10^6$	$2{\cdot}118 \times 10^6$	$7{\cdot}105 \times 10^6$	$110{\cdot}5 \times 10^6$	$34{\cdot}16 \times 10^6$

Thalassiosira gravida	$277{,}501 \times 10^3$	μ^3/litre
Lauderia borealis	$110{,}477 \times 10^3$	
Ditylum Brightwellii	$34{,}164 \times 10^3$	
Chaetoceras compressus	$14{,}701 \times 10^3$	
Asterionella japonica	$9{,}900 \times 10^3$	
Chaetoceras densus	$7{,}105 \times 10^3$	
Rhizosolenia hebetata	$2{,}118 \times 10^3$	
Chromulina pusilla (from Knight-Jones and Walne, 1951)	$4{,}336 \times 10^3$	
"μ-flagellate" (from Table II)	$4{,}664 \times 10^3$	

te: Suffices indicate the number of observations contributing to the mean.)

STIMATES OF DIVISION RATE AND PHOSPHORUS UPTAKE

't of a research programme on the phosphorus uptake of diatoms and μ-flagellates at different ratures has given results for *Isochrysis galbana*, *Chlamydomonas* sp. and *Phaeodactylum*. ations were made on the uptake of phosphorus by these algae from culture media, Harvey's method (1948), with a Spekker absorptiometer. The algae were kept in the for 12 hours in sea water of normal phosphorus content before the experiment began, in to overcome any phosphorus debt (Ketchum 1939); they were taken from cultures starting out 20–30 μgP/litre three weeks previously. Observations on the numbers of algae and e phosphorus content of the medium were taken every four hours for the first day. By me most of the phosphorus had been absorbed and growth was ready to start; a typical ment is illustrated in Fig. 32 (Part V). It was observed that growth was rarely released until of the phosphorus had been absorbed. This observation has also been made on other cultures *Sceletonema costatum* Grèv.). Counts were continued until growth had finished; there is

a genuine lag phase in the growth-rate that seems to be related to the amount of phosphorus can be absorbed, during the absorption period.

The experiments were carried out either in a refrigerator, the temperature of which was constant (to within 1·0° C.) between 6° C. and 12° C. or in a warm bath, the temperature of w was controlled between 14° C. and 25° C. (fluctuation, about 0·2° C.). The light intensities all experiments were kept low, as photosynthesis was to proceed slowly. Phosphorus up varies with phosphorus concentration and with nitrate concentration (Ketchum, 1939), s experiments were started with an excess of nitrate (over 250 μg/litre N) and a " marine " centration of phosphorus (21–44 μg/litre P).

As the phosphorus uptake will depend on the number of plants, we tried to start the experin at the same level of numbers: 100 cells/mm³. This did not succeed exactly, so the final up are expressed in μg-atoms/litre/cell/hr. The initial density was used, because growth in nun never started significantly until all the phosphorus had been taken up.

The results of the series of experiments on three algal species at six temperatures are giv Table IV. It is shown that the uptake of phosphorus by the μ-flagellates is considerably less that of the diatoms. This would be expected, as they are smaller than the diatoms; but sn size seems to be no explanation of the finding shown in the last line of Table IV that they te divide a little more slowly. It must be pointed out that very little is known of flagellate physio and that these experiments might set the flagellates at a disadvantage in comparison wit diatoms (e.g., the excess of nitrate, the continuous light or the 12 hours period in darkness b the experiment). So, the results for the μ-flagellates are not decisive because of the experim conditions; yet, for these experiments, diatoms take up phosphorus more rapidly than flage and subsequently divide more rapidly.

Table IV
Phosphorus uptakes of three algae

Phaeodactylum

Temperature ..	6° C.	8 °C.	10° C.	16° C.	18° C.	20° C
Uptake (μg-at./l)	1·0	1·373	0·656	0·856	1·373	1
Time (*hrs.*) ..	72	30	12	25	30	72
Uptake/hr. ..	0·0138	0·0457	0·0547	0·0342	0·0457	0·
Initial numbers /mm.³ ..	110	108	50	60	108	110
Volume (*ml.*) ..	2,000	2,000	2,000	2,000	2,000	2,000
Uptake μg-at./l/ cell/hr. ..	$6{\cdot}27 \times 10^{-11}$	$21{\cdot}2 \times 10^{-11}$	$54{\cdot}7 \times 10^{-11}$	$28{\cdot}5 \times 10^{-11}$	$21{\cdot}2 \times 10^{-11}$	$6{\cdot}25 \times$

	Chlamydomonas species			*Isochrysis galbana*		
Temperature ..	8° C.	12° C.	16° C.	8° C.	12° C.	16° C
Uptake (μg-at./ l)	0·875	0·547	0·984	0·6875	0·781	0
Time (hrs.) ..	48	48	48	48	48	48
Uptake/hr. ..	0·0182	0·0114	0·0205	0·0143	0·0163	0
Initial number /mm.³ ..	72	110	48	58	190	6
Volume (*ml.*) ..	2,000	2,000	2,000	2,000	2,000	2,00
Uptake μg-at./l/ cell/hr. ..	$12{\cdot}6 \times 10^{-11}$	$5{\cdot}18 \times 10^{-11}$	$21{\cdot}4 \times 10^{-11}$	$12{\cdot}3 \times 10^{-11}$	$4{\cdot}29 \times 10^{-11}$	$11{\cdot}2 \times$

Table IVA
Phosphorus uptakes and division rates of three algae

rature	10° C.	16 C.	16° C.
.. ..	*Phaeodactylum*	*Chlamydomonas* species	*Isochrysis galbana*
µg-at./l/cell/hr. ..	$54{\cdot}7 \times 10^{-11}$	$21{\cdot}4 \times 10^{-11}$	$11{\cdot}2 \times 10^{-11}$
ns/day	0·24	0·17	0·19

indications from considerations of size, numbers, phosphate uptake and division rate, at µ-flagellates may be omitted from calculations of useful production in favour of the more tant diatoms, without introducing errors of the first magnitude.

3. Diatoms

pumps and traps have been used to sample diatoms. Lohmann (1911) found that even when ed fine silk, the small and numerous diatoms were lost through the meshes. However, the diatoms (*Rhizosolenia styliformis* Brightwell, *Biddulphia sinensis* Grèv., and *Coscinodiscus nus* W. Smith) appear to be caught adequately by nets; indeed this might even be true for edium-sized diatoms (e.g., *Ditylum Brightwellii*, *Guinardia flaccida* Castr., and *Eucampia cus* Ehrenburg). For such diatoms, Aikawa (1935), using Apstein's (1896) results, with a et, computed a coefficient of variation of 8·3–17·1 per cent.

catch the small and numerous diatoms Gran (1912) introduced the use of the centrifuge, 1931 Utermöhl brought in the use of the sedimentation method with the reversed microscope. an Nielsen (1938) demonstrated that the numbers of diatoms found by the sedimentation od was often up to three or four times as great as the centrifuged catch. Again, he pointed out he net catch is 1/1000th of the quantity found by the sedimentation method. The coefficient iation of sedimented organisms was estimated by Schmidt-Ries (1936) using diatoms, blue algae, ciliates and gymnodinians; this was always a lot less than that of the centrifuged s. Bernard et Fage (1936), however, estimated that the error between replicate counts of ented catches could be as much as 30 per cent.

as decided to use the sedimentation method for the estimation of the diatoms. Water samples aken at 0·5 m., 10 m., 20 m., 30 m., 40 m. and at the bottom. These were mixed into one , preserved and were counted in 20 ml. samples under the reversed microscope. There was doubt whether all the diatoms would be sampled adequately by such a small volume, so a nternational net was also hauled from two fathoms off the bottom up to the surface at each 1. When the catches were compared, there were more of all diatoms in the sedimented s, with the exception of *Coscinodiscus concinnus*. A comparison as catch in numbers/litre en the two methods was made by putting common diatoms into three groups, " small ", ium ", and " large ". The " small " diatoms were *Asterionella japonica*, *Chaetoceras brevis*, , *Chaetoceras compressus*, *Sceletonema costatum* and *Thalassiosira gravida*; the " medium " ere *Cerataulina bergoni*, Pér., *Chaetoceras densus*, *Ditylum Brightwellii*, *Eucampia zoodiacus nuderia borealis;* the " large " ones were *Coscinodiscus concinnus*, *Rhizosolenia hebetata* and *olenia styliformis*. The Fine Net was assumed to filter the water that passes through its mouth. tio of small diatoms trapped in the water bottle to those caught in the Fine Net is 3·17 (or one freak catch of *Thalassiosira* is omitted; it is unfortunate that so many of the small diatoms ained forms, because a long chain is comparable to a " large " diatom and a short chain to all " one). The similar ratio for " medium " diatoms is 32·3 and for " large " diatoms is Thus a Fine Net catches adequate numbers of large diatoms but it loses too great a proportion rest. There is a discrepancy between the ratios obtained here and those obtained by Steeman 1 (1938); this must be because the oceanic diatoms that he used are in the main smaller and ss tendency to form chains. Analyses of variance were carried out on the comparison of o methods. In these analyses (see Table V) it is assumed that the two catching methods are rable. The variance between the two methods, if so comparable, should not be significant. tches, expressed as numbers per litre, were transformed by logs (Winsor and Clarke, 1940). analysis, there is no regression between the logarithmically transformed mean and variance. as assumed that they were independent.

Table V

Analysis of variance, comparing numbers of diatoms/litre caught by water bottle and fine net. (Main effects nets.) Cruise VI, Sir Lancelot, '49

	SMALL		MEDIUM		LARGE	
	DF	*Mean Square*	*DF*	*Mean Square*	*DF*	*Mean Square*
Groups	4	36·4274	4	11·6076	2	10·3528
Nets	1	253·7872	1	36·0536	1	7·0041
Stations	42	7·6072	42	2·0400	42	1·9383
GN	4	5·3261	4	5·7621	2	2·1890
GS	168	1·9998	168	1·4388	84	0·6201
NS	42	4·3095	42	0·9104	42	0·3546
GNS	168	0·9496	168	0·7791	84	0·3936
S_N^2		1·1604		0·1635		0·0511
Pooled residuals ..		1·0514		0·8980		0·4088

In the analysis, the Main Effects " Groups " and " Stations " are of no interest because vary independently of the difference between the two methods of capture; the estimate of va between the two methods is expressed in the Main Effect " Nets ". Some of the first order actions are not significant, so these are pooled with the second order interactions to give p residual variances. From the pooled residual and the Main Effect " Nets ", the compone variance have been extracted to find S_N^2 (e.g., " Small " diatoms, M. Square " Nets " $= S^2 + 5$ $215\ S_{SN}^2 = 253{\cdot}787$; NS $= S^2 + 5S_{NS}^2 = 4{\cdot}310$; $S_N^2 = 1{\cdot}160$). In Table V, there are three to observe, the Main Effect " Nets ", S_N^2 and the pooled residuals; each variance becomes s as the size of diatom increases.

Combining these results with the comparison of mean catches, we find that for " large " di the gears catch nearly equal quantities and the variance between them (as $S^2 + S_N^2$) is compar small. For the other two groups the " small " and " medium " diatoms, the Fine Net catch $\frac{1}{10}$ or $\frac{1}{30}$ as much as the waterbottle, and the variance between the two gears is three or four ti high as that for the " large " diatoms. This means that the catches of the Fine Net are comp with those from water bottles only when the large diatoms are being caught.

4. Animals

In the sampling of plankton animals, there has been an uncertainty about which gear to use possible to use a net, a pump or a trap, and of nets one may use vertical or horizontal ones. F the use of a flowmeter in a plankton net is open to doubt, because it is theoretically unnec The following discussion sets out the reasons for using a vertically hauled net with a flowm

(*a*) ON THE USE OF PUMPS, VERTICAL AND HORIZONTAL NETS

Comparison between net and pump have usually shown that animal species are caught same proportions and in about the same quantities (Forel, 1874; Fordyce, 1901; Bachmann Robert, 1922; Ricker, 1932; Gibbons and Fraser, 1937; Pyefinch, 1949; Wiborg, 1948). (1932) showed that the errors of pump collection are comparable to those of net collection. demonstrated by Barnes (1949) that the coefficient of variation of the water volume of a pum in a replicate series was about 4 per cent, whereas the coefficient of variation of the num plankton animals in the same series was 28–31 per cent. Pyefinch (1949) wrote that the pum to damage animals. In any case, pumps are hard to manage, maintain and operate, as Robert p out in 1922. It appears that the only advantage of a pump lies in the fact that the wate from any given depth can be measured; this can be done, if necessary, by putting a flown the net.

sources of error in net collection have been considered by many writers on plankton. These summarized in the following way. Robert (1922) found that the filtering surface of the silk ıced by 50-100 per cent merely by wetting it; Ricker (1932) reduced the variance of the s in his replicate series by drying the net between hauls, and then he further reduced it by also g the net with soap and water. Hensen (1887) and Künne (1933) wrote that a Hensen egg ɔuld be hauled at 1 m./2-3 sec.; above this speed I have shown, with a flowmeter, that less is filtered. Buchanan-Wollaston (1914) introduced the use of a counterweight, which ted the spill of catch with the ship's rolling and also provided a very steady hauling speed, the ship's rolling.

ıy estimates of the error due to the net and the error due to the distribution of the plankton een made by the use of replicate hauls. The coefficients of variation for vertical hauls may ɐn first. Aikawa (1935), using Apstein's 1896 data with an Apstein net gave coefficients of ɔn for " copepoda " as 35 per cent. Sir William Herdman (1921) carried out seven series vertical replicates each in calm weather, each always at slack water and each at a different year. The results are given in Table VI; the probable errors of the means given by Herdman h species have been converted to coefficients of variation.

Table VI

Coefficients of variation from Herdman's Probable Errors
(Percentages, v. Herdman, W., 1921)

Coscinodiscus radiatus, Ehrenburg ..	16	38	37	24	70	59	38
Ceratium tripos, Müller	18	32	21	25	57	35	29
Pseudocalanus elongatus, Boeck ..	19	30	24	41	28	16	37

ɔor and Walford (1936) derived a coefficient of variation for the Hensen egg net of 24·6 per Vinsor and Clarke (1940) found that Gardiner's (1931) data on the Standard International ded a coefficient of variation of 43 per cent, and that Künne's (1933) data on the Hensen egg l Helgoland larva net combined gave a coefficient of variation of 47 per cent. Barnes (1949) a coefficient of variation of 25 per cent for a Standard net hauled vertically. Herdman's es tend to be in the main smaller than the more recent ones; I think that this is because he ed his species in analysis. Denoting the variance by S^2, the estimates of the standard on in Winsor and Clarke's work is usually $\sqrt{(S^2(\text{Hauls}) + S^2(\text{Groups} \times \text{Hauls}))}$; admittedly, S^2 is the appropriate residual in the analysis, but it does contain error contributed by the ɔus assemblage of groups in the sea, which in the present context is not relevant.

·native methods to the vertically hauled net are oblique nets or a series of horizontal nets. · and Clarke (1940) quote a coefficient of variation of 31 per cent for a replicate series of : hauls, and Silliman (1946) gives coefficients of variation that vary between 44 per cent and · cent. Horizontal nets according to Winsor and Clarke (1940) yielded coefficients of variation ·24 per cent, and according to Saville (1949) of 69 per cent; however, Barnes (1951) has quite ·/ reduced this to 38–48 per cent by the use of a kite to make the net hold its depth constantly. very interesting to see how Hensen (1887) tackled the problem of which form of net to use; lysis was not one in use today, for to cover the range of numbers he used the mean deviation ıe geometric mean, expressed as a percentage. Fifty-three pairs (or triplicates) of vertical ·ith the " Plankton-netz " yielded a mean deviation of 14 per cent; ninety-one pairs (or es) of horizontal hauls with the same net yielded a mean deviation of 28·6 per cent. These tions were taken at all seasons.

this summary it appears that vertical nets give an estimate that is somewhat more accurate ıorizontal net or an oblique net. Vertical nets are, of course, much easier to handle, consume e on stations and at the moment produce less labour in working up the results; they can ch a larger sample in the same time, because larger nets can be used in this way. It is in true that an increase in the size of sample leads to a reduction in the variance.

THE USE OF A FLOWMETER IN VERTICALLY HAULED NETS

·etically, and this was probably Hensen's view, a flowmeter is unnecessary. The virtue of cated cone at the mouth of the net lies in the fact that only that quantity of water is allowed

in the net that can be filtered away by the net surface. Hensen established filtration coeffic for various sizes of silk mesh and for various water pressures; he showed that a conical ne more efficient than a cylindrical one, and worked out the dimensions of a truncated con and the correct hauling speed for it from his experimental data. Harvey (1948) by usi flowmeter, demonstrated that Hensen's egg net filtered the theoretical quantity of water hauled at 1 m./2 sec. Thus to know the volume of water filtered, it should only be nece to know the area of the mouth of the net and the distance through which the net has hauled.

The distance through which the net has been hauled is, however, only known on those paratively uncommon occasions when the net is hauled exactly vertically. Usually the net c up at an angle, which may be very great when wind and tide are opposed. This means that water is being filtered than expected. Here is the use of the flowmeter: the net can be haul practically any weather, as the volume of water filtered is measured and not estimated fro length of rope out. However, Whiteley (1948) and Silliman (1946) have tried to estimate the of a flowmeter and have come to the conclusion that it makes very little difference.

A practical attempt has been made to find whether a flowmeter is worth using or not. Simpson, who has very kindly allowed me to use his results, has carried out plaice egg crui January, February and March from 1947–50; triplicate Hensen hauls were taken at each st and during the two cruises that I have used, Harvey's flowmeter was employed. These c (I and II, Sir Lancelot, 1949) were carried out in the Flamborough area; they were com during the worst weather in the year. Before embarking on these cruises, Mr. Simpson calib the flowmeter in Yarmouth Roads and found that 1 metre of depth hauled on the rope ga revolutions on the meter wheel.

After it had been counted, the material was treated in two ways. The first was the trad method by which it is assumed that the net filters $\frac{1}{3}$m.^{3} per metre of depth through the net is hauled; in the second method, the values of the flowmeter readings (redu metres) were substituted for the value of " metres hauled ". The two sets of results fo animals and plants are numerically quite different, although they are obviously in other re the same.

Before we analyse the results, the question could well be raised that the triplicate net haul not in fact replicates, because two nets were used alternately. Similarly, these two nets w different ages, and perhaps of different degrees of shrinkage, etc. The net samples were against each other, using the t-test to find if the populations of the three samples were the this was carried out on ten animal groups, testing Net I against Net II, Net I against Net I Net II against Net III. In none of the 24 comparisons was the 0·05 point of probability ex (DF = 36). Thus it is reasonable to treat these nets as triplicates. The groups used were *finmarchicus*, ♂, ♀, and copepodite stage V; *Pseudocalanus elongatus*, ♂, ♀, and juvenil *Paracalanus parvus*, ♂, ♀, and juveniles.

It would be possible to show whether a flowmeter should be used by comparing the revo found under different conditions of wind and tide with the expected number of revolution exactly vertical haul. I used an indirect method because I wanted to find not only the re in the estimate of numbers, but also any change in the variance.

The use of the flowmeter will be examined in three stages. First, its effect in altering the e of numbers: secondly, its effect on the variance of the estimate of numbers; and thirdly, its bad weather will be discussed.

The numerical effect of the flowmeter is estimated by the use of an analysis of variance th of which is set out in Table VII. Only two nets were used because it was easier to make th of comparison with two, rather than three. The analyses were carried out for four animal on catches /m.^{3}, transformed by logarithms. The results are given in Table VIII. The Mai " Flowmeter " is an estimate of the variance between " With flowmeter " and " No flow across the net differences. If we take one form of result as standard, e.g., " No flowmeter the variance given by this Main Effect expresses the numerical factor of the flowmeter. T coefficient of variation derived from this variance is an estimate of the proportionate ch estimated numbers due to the use of the flowmeter. Because the flowmeter measures a quantity of water filtered in a non-vertical haul, it can be assumed that the change in es numbers is a decrease; if a greater quantity of water is filtered, a given catch in the net r expressed as a smaller quantity per unit volume. In fact, the mean of numbers in " With flow

in the analysis is considerably less than the mean of numbers in the " No flowmeter "

Table VII
Form of analyses for estimation of flowmeter effect

ations	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Flowmeter, II																						
owmeter, III																						
owmeter, II																						
Flowmeter, III																						

Table VIII
Analyses for estimation of flowmeter effect

	Paracalanus parvus juvs.		*Calanus finmarchicus* ♀		*Calanus finmarchicus V*		*Pseudocalanus elongatus* ♀	
	DF	MSq	DF	MSq	DF	MSq	DF	MSq
ıeter	1	0·3046	1	1·2201	1	0·5809	1	0·8129
.. .. ..	1	0·1420	1	0·1688	1	0·0563	1	0·1200
ction	1	0·0001	1	0·00015	1	0·1005	1	0·0042
duals	84	0·1342	128	0·0822	136	0·3324	56	0·0938
cient of variation from n Effect Flowmeter ..	15·4 per cent		35·2 per cent		14·8 per cent		42·9 per cent	

e Main Effect " Flowmeter " makes the comparison between the two nets when used with vithout the flowmeter. It is obvious from the results (see Table VIII) that the interactions are ignificant, and before going further these were pooled with the " Individuals ".

r *Paracalanus parvus* juvs. and *Calanus finmarchicus V.* the Main Effect " Flowmeter " was gnificant, but it was so in the case of the other two animal groups. From these it is legitimate .imate coefficients of variation; they are shown to be quite high. They were also estimated ıe two non-significant animal groups. In view of the logarithmic transformation, these ates of significance and variance are not exact, but they show the order of the effect. Thus ay say that the flowmeter has reduced estimates of numbers by factors of between 15 and r cent.

: the second stage in the work on the use of the flowmeter, an analysis of variance was used mpare the results when the flowmeter was used with those when it was not, in order to find he flowmeter affected estimates of variance. The catches/m.^{3} were transformed by logarithms der to normalize the distributions (Winsor and Clarke, 1940). This did not succeed com- y in this case, because there was still a slight regression between the mean and variance. The priate transformation is likely to be an inverse sine type (Anscombe 1948, 1950) and is complex olication. The logarithmic transformation was used as no estimate of significance was made o numerical conclusion drawn from the magnitudes of the variance. Three factors are used tions, Groups (species, sexes or stages of animals and plants) and Nets (triplicate hauls). econd order interaction is used as a residual; first order interactions that are not significant ooled with the second order interaction to form a residual (Table IX). As we are at the moment nterested in the effect that the flowmeter has in reducing certain mean squares, there is no in carrying the analysis further than the mean square.

Table IX

Analyses of variance to show the effect of the flowmeter in reducing the variance of an estimated number of zooplankton

	Cruise I Sir L. '49			Cruise II Sir L. '49			Cruise II Sir L. '49 Animals			Cruise II Sir L. Plants		
	DF	*With Flowmeter*	*Without Flowmeter*	*DF*	*With Flowmeter*	*Without Flowmeter*	*DF*	*With Flowmeter*	*Without Flowmeter*	*DF*	*With Flowmeter*	*Wit Flo me*
Stations ..	21	2·8125	3·4666	36	2·5701	2·5029	36	1·1009	0·8960	36	3·2438	3·8
Groups ..	7	4·5723	5·2615	13	6·2062	6·8077	9	4·6308	6·0141	3	2·5992	2·6
Nets ..	2	0·6127	0·7866	2	0·0487	0·3144	2	0·0929	0·2254	2	0·0964	0·1
NS	42	0·1496	0·1837	72	0·6007	0·8261	72	0·3137	0·4431	72	0·5234	0·6
GN	—	—	—	26	0·3056	0·3588	—	—	—	6	1·0364	1·1
GS	147	0·5271	0·6215	468	0·6673	0·8038	324	0·3107	0·3936	108	1·3680	1·5
GSN ..	308	0·1189	0·1402	936	0·1406	0·1720	666	0·0805	0·1062	216	0·2888	0·3

(*Note:* Non-significant first order interactions are left out and the second order interaction is a residual.)

In the four examples given the use of the flowmeter produces a reduction in the Main E " Nets " and in the residual error. It is a corollary that the first order interactions are als reduced by the effect of the flowmeter. The reduction in the mean square for the Main Effect " N is greater in Cruise II than in Cruise I. The weather was very much rougher in Cruise II than experienced in Cruise I. This is where one would expect the flowmeter to become useful. comparison is effective on different treatments of the same population. It may be concluded the use of the flowmeter significantly reduces the estimate of numbers as caught in a Hensen and also significantly reduces the variance of that estimate.

At one stage in this work it was thought that bad weather in itself might have an adverse on the use of the flowmeter. Cruise I, Sir Lancelot, 1949, was not carried out in continuous weather; in fact, in a number of hauls the net was allowed to come up vertically; there were, how many other hauls when the net came up at angles of up to 30 deg. from the vertical. The effect wind was estimated by dividing the stations into those at which the wind strength was " F and below " and those at which the wind strength was " Force 4 and above "; the first in the light airs, moderate breezes, that blow over slight seas, but the second includes only the winds that whip up fairly heavy seas. Analyses were carried out in the same way as in Tab (see Table X). Where necessary, the first order interactions were pooled with the second interactions to give a new residual in all four analyses; it happens that the first order inter between Groups and Stations is the only significant one. The table is considerably shorten showing only the relevant effects—the Main Effect " Nets ", the Residual and the significa order interaction, Groups × Stations. There are two possible comparisons—that between " flowmeter " results and " Without flowmeter " results, and that between the " Wind " station the " No wind " stations. It must be pointed out that in the flowmeter comparison the biol populations were identical but that in the wind comparison the populations were unavoi different. This means that a comparison between " With flowmeter " and " Without flowm is quite valid, but that the comparison between " Wind " and " No wind " results is not neces valid.

Table X

Cruise I, Sir L., '49: flowmeter treatments compared at " calm " stations and " windy " stations

	WIND				*NO WIND*			
	With Flowmeter		*Without Flowmeter*		*With Flowmeter*		*Without Flowmeter*	
	DF	*MSq*	*DF*	*MSq*	*DF*	*MSq*	*DF*	*M*
Nets	2	0·0156	2	0·0716	2	0·0943	2	0·0
GS	16	1·1424	16	1·3848	10	0·4064	10	0·5
Residual	52	0·0232	52	0·0852	34	0·1526	34	0·1

e flowmeter comparison in Table X yields the following points. A reduction in mean squares is ed by the flowmeter for the " Wind " stations; this is shown in Main Effect " Nets ", the first Interaction Groups × Stations (GS) and also in the residual. This is of much greater degree the perhaps comparable reduction for the whole cruise given in Table IX. There is no reduction e mean squares effected by the flowmeter at the " No wind " stations. Thus the comparison een the " Wind " and " No wind " results lies in the difference between the degrees of reduction ean Squares by the flowmeter. This is the best way of comparing the " Wind " and " No " stations, because any difference in variance between these sets of stations could be attributable e fact that they are concerned with quite different biological situations, but the flowmeter should have no relation to the two populations. The conclusion is that the flowmeter is more l in heavy weather, because a reduction of about four times in the variances is achieved, een " Without flowmeter " and " With flowmeter " at the stations carried out in strong wind. e residuals for the " No wind " stations were much greater than those for the " Wind " stations. ough little meaning should be attached to this, there was enough to arouse curiosity. Cruise I, ANCELOT, 1949, was then divided into three groups: (1) stations at which the rope angle was al; (2) stations at which the rope angle was 10 deg. from the vertical; (3) stations at which the angle was 20 deg. from the vertical. This is only a rough index of the drift of the ship due to or tide, but it can be safely written that the effect of tide on the rope angle will not be great s there is a quite strong wind blowing against the tide. Three analyses were carried out, given ble XI.

Table XI

Cruise I, Sir L., '49: mean squares nets and error for *Calanus finmarchicus* ♀ are compared for different wind strengths as estimated by the angle of the rope

	ROPE ANGLE 0°		10°		20°	
	DF	*MSq*	*DF*	*MSq*	*DF*	*MSq*
Stations	4	0·1017	4	0·2779	3	0·1616
Nets	2	0·1721	2	0·0333	2	0·0046
Error	8	0·0496	8	0·0208	6	0·0166
Total	14		14		11	

ere are two remarkable points about this table: first, that the Mean Square *Error* is reduced ree times as the rope angle is increased, and secondly, the Mean Square *Nets* is reduced by t fifty times in the same series. This cannot be an effect of the gear, but must be caused by the bution of the animals. The results of replicated hauls do not conform to the Poisson distri- n, hence it is usually concluded that plankton animals are found in clumps or groups. It is ole that these groups are to some extent broken up by wind-generated turbulence.

e conclusion from this work is that a truncated cone of the sort that Hensen designed, when d vertically, on a counterweight system and used with a flowmeter, will give as accurate an ate of the general animal plankton for the least amount of labour as we can obtain. The use rizontal nets means that they must be towed at all levels for a longish period—up to half an if a number of net hauls are to be counted I would prefer to replicate a vertical haul and then e the sampling error by the reciprocal of the square root of the number of replicates. If this e with a bundle of nets there is not so much loss of station time as there is if horizontal nets ed.

5. Techniques used in Planning the Cruise Grids and in Working up the Results

ext stage in the process of estimating the plankton populations was in the cruise planning. ea to be used was that of the Shields fishery, which extends up to 50 or 60 miles in the seaward on from Shields. A reconnaissance series of cruises in 1948 had shown that patches exist in a that could be easily covered by a grid of stations extending seawards about a hundred miles t normally to the coast between Whitby and St. Abbs' Head. This is the grid mentioned in . Along the latitudinal lines of the grid, stations were made at distances of 15 miles; the lines elves were set 25 miles apart. At each station, one Hensen net and one Fine net were hauled he bottom to the surface, and water-bottle samples were taken at 0 m., 20 m., 30 m., 40 m., the bottom. It was intended to carry out these cruises from south to north, but the weather,

fuelling and the necessity to search for the patches did not always allow this. Five cruises completed—VI, VII, VIII, IX and X, Sir Lancelot, 1949; the last was designed and carried Mr. Wimpenny for his N.E. coast fat estimations, but he has kindly allowed me to use the g plankton results. The station grids with numbered stations are shown in Fig. 10 (Part III). time of these cruises the Decca navigator was operating from two stations only; this meant t the northern end of the grid the angles between the lines became very acute and the possibi error became great. Captain T. A. Sutton, Master of the Sir Lancelot, devised and used a s chart which combined the Decca navigator signals and those from the Direction Finding Sta this reduced the error of navigation considerably.

The large samples taken by vertical nets are dealt with in the laboratory by some form c sampling. This may be used on condition that the error due to sub-sampling is less than th to sampling. Errors in sub-sampling have been considered by a number of workers. Harc Gunther (1935) have shown that the mean deviation was 22·4 per cent for " medium calan Littleford, Newcombe and Shepherd (1940) found that clumping may occur in the use of a Sed Rafter cell; this was denied by Gilbert (1942) who found that the distribution of sub-sa phytoplankton approximated closely to the Poisson series.

Two samples (each containing six species) were sub-sampled ten times by the same op the method was that devised by Hensen (1887) (whirling flask and Stempel pipette). Wh means of the twelve sample groups were plotted against their standard deviations, the rela Fig. 3 was found. It is clear that the standard deviations are not randomly arranged with to the mean, but that there is a regression of standard deviation on mean. Inspection of leads one to believe that the appropriate regression would be curvilinear and that theref question of the significance of the fit of a linear regression is a meaningless one. Transfor to logarithms produced the relation given in Fig. 4; a regression is again shown and in this c

Regression of standard deviation on the mean, in replicated plankton sub-samp

Fig. 3.
A whirling flask and stempel pipette was used.

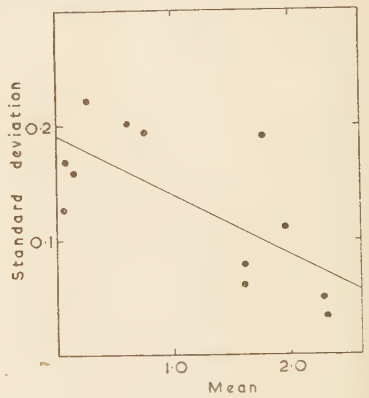


Fig. 4.
Transformed by logarithms.

linear regression is significant. However, by the use of this transformation the range of deviations for the same means is reduced from 50 × to 4 ×. The logarithmic transfor not the appropriate one. As the purpose of the following analysis of variance was only to the main sources of error, the search for the appropriate transformation was taken no fu

The following analysis was carried out:

Table XII

Analysis of variance on sub-sampling carried out on two samples ("copepods", "dead co *Biddulphia regia, Cumacea, Chaetoceras densus, Coscinodiscus concinn*

	DF	*MSq*
Groups	5	17·1871
Replicates	9	0·0250
Samples	1	0·2025
GR	45	0·0221
GS	5	0·0333
RS	9	0·0116
GRS	45	0·0226
Residual	104	0·0219

) interaction was significant; the Main Effect Replicates was not significant when compared the residual or second order interaction, and that due to Groups and Samples is not interesting; e the coefficients of variation from the residual term can be used directly; for the " copepods " ' dead copepods " they are 17·3 per cent, 13·2 per cent, 62·5 per cent and 50·0 per cent, giving an of 35·7 per cent. This error is included in all estimates of numbers and in all methods of ɔuring.

the laboratory the samples were sub-sampled in a whirling flask and counted. The samples finally estimated as numbers below one square metre and as numbers per cubic metre. The first ed for an estimate of numbers in the area and the second is used for work on the aggregation e herring—because the fish may be interested in densities and not in numbers. It was clear in 948 cruises that patches of animals and plants occurred and that these were easily contoured Buchanan-Wollaston (1926) and Savage and Wimpenny (1936) had shown. Against this, ever, there was the question of plankton patchiness—the patchiness within small distances that it easily falsify any contour arrangement.

scussion on this patchiness began with Haeckel's (1891) criticism of Hensen's work. Hensen quite aware, even in 1887, of the patchiness in small degree, that since his time has become so documented. He attributed this to reproductive processes and said that it would be minimized aking vertical hauls; in this he was clearly influenced by the recent discovery of plankton ification by Chierchia (1885) and Chun (who published his results in 1887). The quarrel with ckel may have developed from the use of the word *gleichmässigkeit*. I think that his meaning of the regularity (not uniformity) that may be sampled adequately at stations distant from one her.

ıe argument was carried a stage further by Hardy (1936) in the use of the automatic plankton rder. In this paper a number of figures are given in which wide variations of numbers of kton organisms are shown to occur quite close to each other. In each instance the recorder towed over great distances.

ıe same argument was in the minds of freshwater biologists. Much of the work carried out in Swiss and Bavarian lakes depended on the use of a single station in a lake. Naber (1933), g a 2-litre plankton trap, took four hauls rapidly at one station and then eight hauls scattered the area of the lake; he found that there was, however, no significant difference between the ıs of the scattered hauls and the means of the replicates at the central station. Ricker (1937) the same sort of method, but he employed the ratio of the variance to the mean to detect the ence of clumping. (This ratio should be unity if the plankton distributions follow the Poisson s.) Forty per cent of the organisms occurred in distributions that departed significantly from mplied Poisson distribution. In 1945 Baldi, Cavalli and Pirocchi found a significant departure ı the Poisson distribution in the horizontal arrangement of plankton animals. Baldi, Buzzati-erso, Cavalli and Pirocchi (1945) demonstrated quite clearly that there were distinct popula- of *Diaptomus laciniatus* in Lake Maggiore; this was done by taking many measurements on y individuals and by using a form of discriminatory analysis on the results. The result has been repeated many times by the workers at Pallanza under the late Professor Baldi.

tchiness within small areas in which variations in abundance are not great is described by the of contagious distributions. In the complexes so described, variations in numbers are due to andom distribution of groups and the random distribution of numbers within groups. In the *nus* cruises of 1949, there were, however, wide variations in abundance between stations; as ruises were arranged to show a large patch, these variations in abundance were in addition to random variation of groups and numbers within groups. Thus it was possible to confuse nces in grouping with variances in abundance.

order to estimate the numbers of plankton organisms in the area, it was decided to contour distributions on the cruise grids. The contouring of plankton numbers is not new; Buchanan-aston started to do it in 1916 and Savage and Wimpenny (1936) were able to describe the th of a population of *Rhizosolenia styliformis* by means of it. In both cases, estimates of bers were made. It was necessary to set the contour levels far enough apart so that it was ely that a sample appearing between two contour levels should derive from a population value de these levels; thus, values within the same level are not significantly different and values that eparated by two levels are significantly different. This method is described in detail in Cushing 3). It is on the basis of this procedure that the charting of plankton patches was attempted. areas of the patches were measured with a planimeter; these values were multiplied by the

numbers at each contour level. The estimates were then added for each level, to give estim numbers.

The following summarizes the various methods used for different organisms. μ-flagellat not ignored, but in 1949 it was quite impossible to estimate them adequately at sea; the re gap in the *Calanus* food chain is small. Diatoms were estimated from mixed water sample 0–40 m. and the bottom; *Coscinodiscus concinnus* and *Rhizosolenia styliformis* were estimate Fine Net samples. Animals were estimated with one Hensen net at each station; a flowme used. We have seen that this is particularly useful in rough weather, and it also appears t errors of sampling are somewhat reduced in rough weather. This may well be because the in which plankton animals are assumed to live may become broken up in the turbulences o seas. The numbers of diatoms are expressed as numbers underneath 1/100m.^{2} and the ani numbers underneath 1 m.^{2}. These numbers are plotted on station grids and are contou Buchanan-Wollaston's method (1926); the contour levels are set apart by the use of con limits attached to one or more observations. Thus, the first stage in elucidating the dynam has been reached—the accurate estimation of numbers in plankton populations.

Part III

Plankton Patches and their Identity

1. Introduction

particular value of estimating the numbers of animals in a patch by contouring arises when a s of observations can be made on that patch during a period of time and so the rates of change umbers may be observed. Up to the present this has been impossible, because water masses ot be marked easily and their rates of movement in shallow seas can only be measured with difficulty. The idea of marking a plankton patch by means of some of its constituent plankton nisms is not new; it was the basis of Wimpenny's (1936) work on the sizes of diatoms. In this on, a method of marking such a patch will be developed; the identity of the patch between es will be made by establishing a constant size difference between those animals within the and those outside it.

nt patches and animal patches will be described. Their identity will be found to imply a south- movement, which will be sustained by the examination of the phosphorus distributions of es VI and VII.

will be shown that the differences in size characteristic of the patches are not due to the presence *alanus* " *helgolandicus* ". It will be assumed that the copepodite stages of *Calanus* moult een cruises; as this would mean once every 13 or 17 days, it is not unreasonable. From this deration, age distributions for the identified group of patches will be made. The movements e patches in detail will be described; this will also depend on the assumption that the copepodite s moult every 13–17 days.

2. Plants

ISTRIBUTION

s reasonable to believe that plant patches are only regular and consistent in shape when grazing nited; and it can be shown that the large patches of *Thalassiosira gravida* and *Asterionella ica* that are a predominant feature of Cruise VI (see Fig. 5) have become irregular in shape, liminished in size, in Cruises VII and VIII. The effect of grazing by the animals is still limited uise VI and the patches are regular in shape, as if numbers of diatoms had been reproducing me time from a centre. This implies that there was an original patch before rapid reproduction d; the patch shown in Fig. 5 could be an effect of the reproduction of the initial numbers. ing useful is found in charts of plant distributions for the later cruises, and these therefore are cluded in this paper.

. 5 shows the spatial distributions of the commoner diatoms in Cruise VI, expressed as numbers neath 1/100 m.^{2}. μ-flagellates were not sampled and dinoflagellates were present only in numbers. The diatoms are all common ones and are all to be expected in this area. The ational Cruises (1904–07) showed that eight of these diatoms were caught in this area in Lucas (1942), using the continuous plankton recorder, found that in April and May of 1938 939, along the western ends of the plankton recorder lines L, K and A, the following diatoms present: *Lauderia borealis*, *Rhizosolenia hebetata*, *Thalassionema nitzschioides*, Grünow, *oceras decipiens*, Cleve and " *Thalassiosira* ", Grøntved (1952), reporting on the diatoms the 1947 International Cruises, showed that *Asterionella japonica* and *Sceletonema costatum* imited to a very narrow coastal stream. *Chaetoceras compressus*, *debilis*, Cleve and *subsecundus* .) Hust. were found within 70 miles of the English coast. *Thalassiosira gravida* was placed lly in the North Sea, just north of the Dogger Bank.

re are three plant systems, shown in Fig. 5, each with a dominant species, as given in the ing table (dominant underlined).

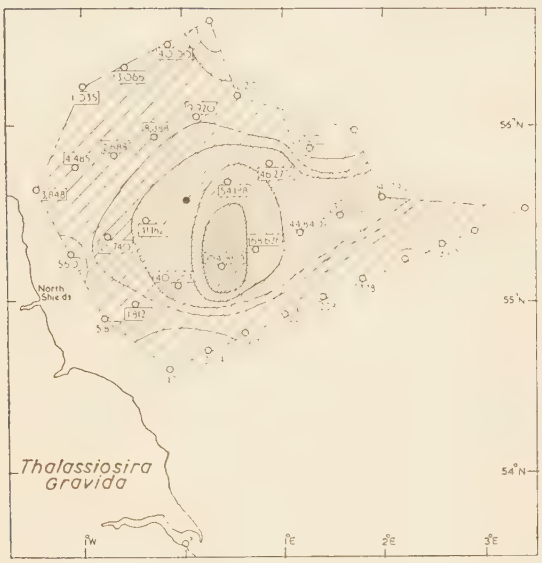
FIG. 5. DISTRIBUTION OF SOME COMMON DIATOMS OFF THE NORTH-EAST COAST IN APRIL

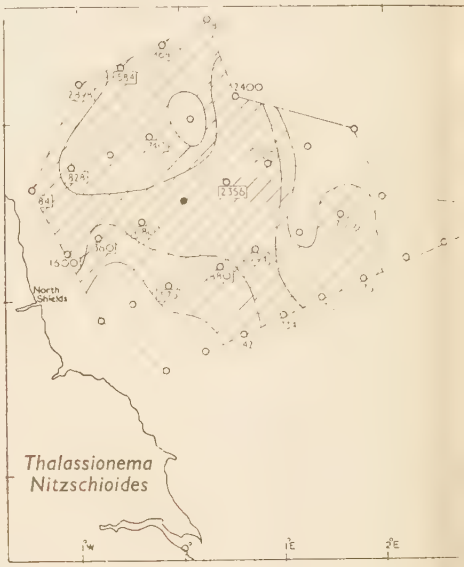
Stations are marked at open circles; at the station marked with the black circle no sample was taken. T
species are arranged in three groups:

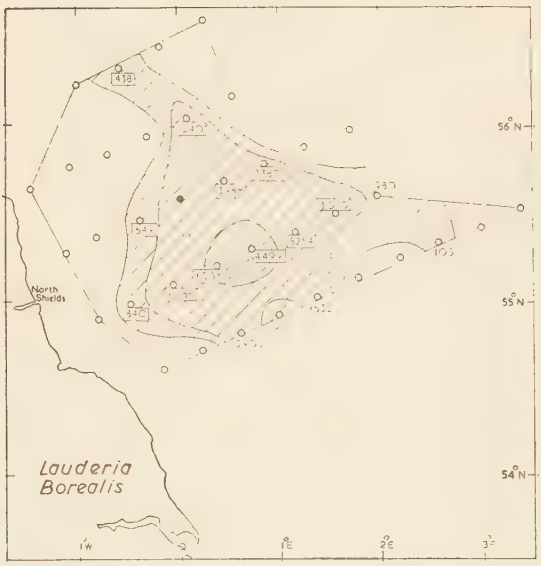
(*a*) *Thalassiosira gravida,*
Thalassionema nitzschioides,
Lauderia borealis,

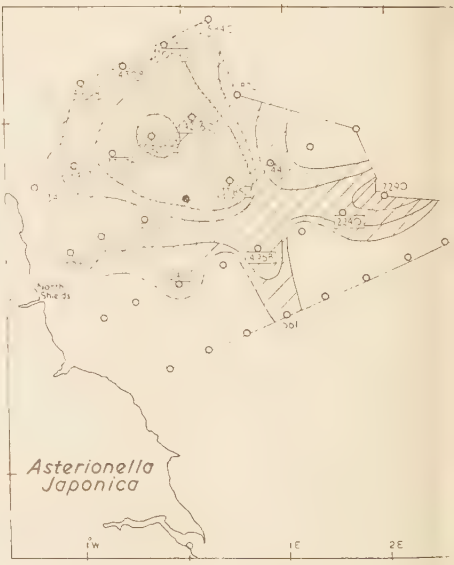
(*b*) *Asterionella japonica,*
Chaetoceras compressus,
Chaetoceras brevis,
Sceletonema costatum,
Ditylum Brightwellii,

(*c*) *Cerataulina bergoni*
Rhizosolenia hebeta
Rhizosolenia Stolte

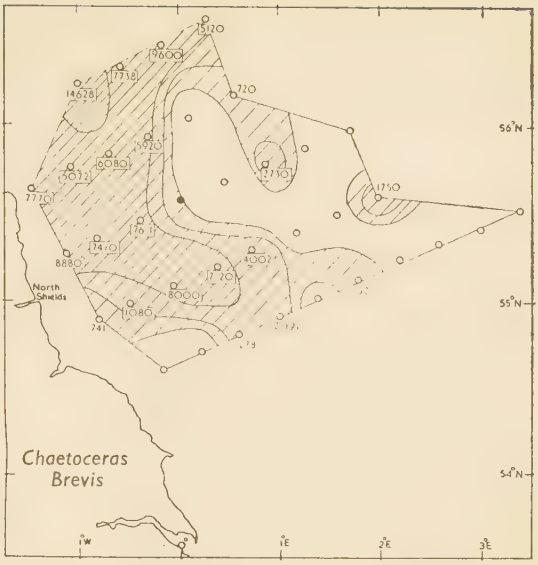




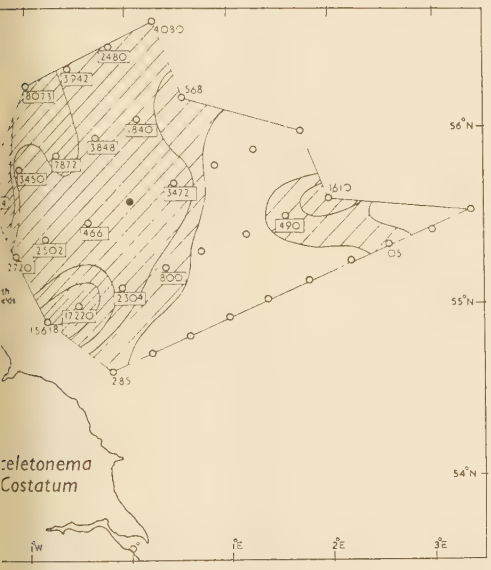




etoceras
mpressus

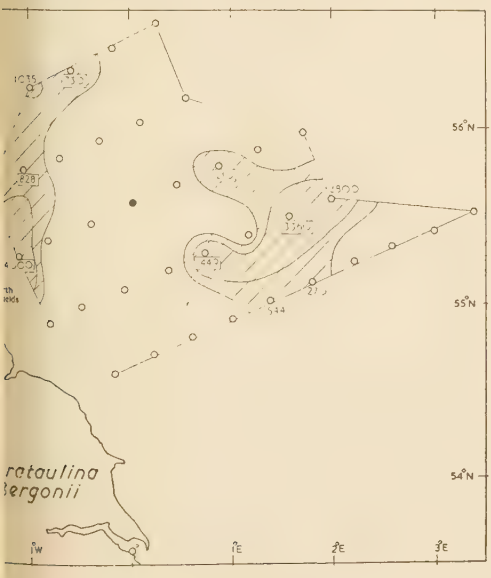


Chaetoceras
Brevis



celetonema
Costatum

Ditylum
Brightwellii



rataulina
ergonii

Rhizosolenia
Hebetata

Table XIII

Diatom communities with dominant species; Cruise VI, Sir Lancelot, 1949

Thalassiosira gravida	*Asterionella japonica*	*Rhizosolenia hebetata*
Thalassionema nitzschioides	*Chaetoceras brevis*	*Rhizosolenia Stolterfothii Pér.*
Lauderia borealis	*Chaetoceras compressus*	*Cerataulina bergoni*
	Ditylum Brightwellii	
	Sceletonema costatum	

In 1948 there was a somewhat similar arrangement in April, in that there was an East a Western area; *Rhizosolenia hebetata*, *Rhizosolenia styliformis* and *Cerataulina bergoni* the east out towards the centre of the North Sea, and the small diatoms were in the west, the coast. This is the same arrangement that Grøntved (1952) has shown from the Inter Cruises of 1947.

(*b*) RELATION OF PLANTS TO PHOSPHORUS IN THE SEA

Phosphorus estimations were made on water samples taken from 0 m., 10 m., 20 m., 30 at the bottom. These estimations were made at sea as soon as possible after the station w pleted. The values from 0 m., 20 m., 30 m. were averaged, and this mean was called Mean Phosphorus, as it is likely to be that value to which the plant distributions are related. Th butions of Mean Surface Phosphorus in μg-atoms/litre for Cruises VI and VII are shown in and 7. These distributions are contoured by the methods described for plankton organ Part II (5).

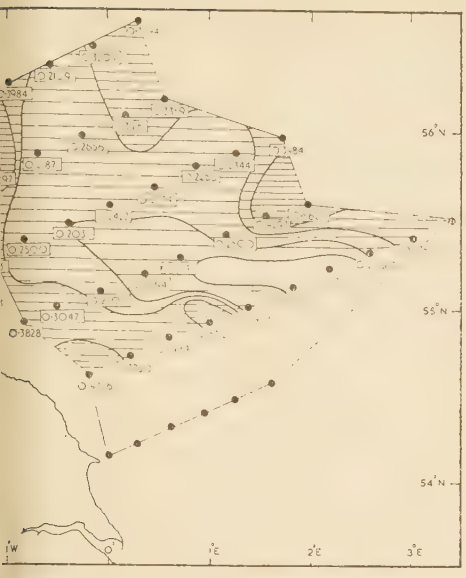
(i) *Method of phosphate determination.* A description of the method of phosphate determ used with its errors is necessary. The requirements in the method were threefold:

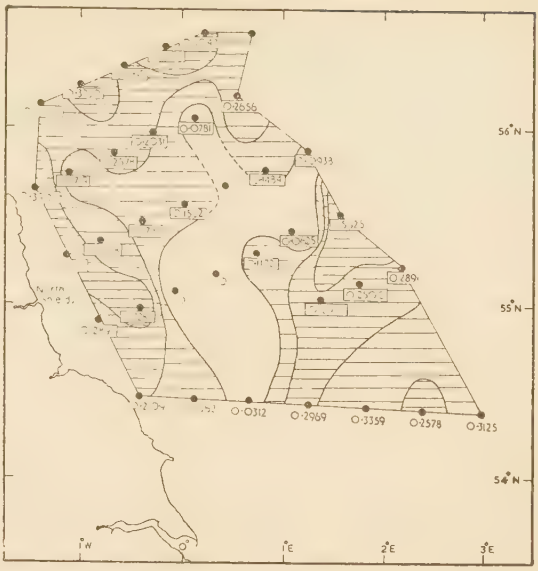
(*a*) that there was no visual comparison, because of sea sickness (cf., Graham, 1936);

(*b*) the galvanometer of the photoelectric method must be eliminated because gimbal tables do not al motion of a trawler sufficiently;

(*c*) the method had to be carried out at sea because at the time of planning there was no adequate m preservation of phosphorus samples.

The colorimeter developed by Roberts (1950) has but one photocell and this operates a ammeter; all the theoretical defects of this system were realized and the risk taken, as no othe had then been developed for this purpose (Ford, 1950). A calibration curve was prepared with phosphorus standards; the instrument was calibrated every day at sea with similar sta This means that the fluctuations in the photocell from day to day were controlled. When t is first turned on, the response of the photocell increases to a maximum after about three m consequently, the light was turned on for five minutes before any determinations were





. 6. Cruise VI, Sir Lancelot, 1949 Fig. 7. Cruise VII, Sir Lancelot, 1949

value is the mean of samples taken at 0 m., 10 m., 20 m., and 30 m., expressed as μg-atoms P/litre.

r point is that the observation tube always had to be put in exactly the same position, or t areas of the photocell were illuminated and different responses obtained. The light y of the lamp was kept as constant as possible by the use of a variable resistance and a ter; as the ship's voltage was variable, this was very necessary.

chemical method was that recommended by Harvey (1948) with one exception. All readings ken after a constant time interval of 15 minutes; we did this because there was a large number ples and it was more practical at sea to treat them in a uniform manner over the rather long involved. As the degree of colour development varies with the phosphorus concentration nstant temperature, for a constant time interval (Berenblum and Chain, 1938*a*, 1938*b*) this practical procedure. In point of fact, as the laboratory temperatures varied only between nd 21·9° C. (and these are extreme measurements), maximum colour development was ly reached (Harvey 1948).

t samples were dealt with within twelve hours; twenty-four hours was the maximum time l to lapse before determining their phosphorus content. As the pressure of time was rather n increment check as recommended by Harvey (1948) on each determination was not used. or on the calibration graph was about 1 μg/litre at its maximum; salt error was estimated e graph using Cooper's (1938) factor of 1·19, and this was checked by separate salt error ions carried out at sea.

rrors in method. The faults in this method are the use of a single photocell and the lack of ement check. The errors were estimated in the following way. Three sea-water samples t up, one enriched with much phosphorus (labelled (*c*) in Table XIV), one depleted of orus by diatoms (labelled (*a*) in Table XIV) and one only partially so depleted (labelled able XIV). Ten replicates were estimated on each of these samples in the laboratory ashore, s far as possible the methods that we had used at sea. The results of this experiment are in Table XIV.

Table XIV

Coefficients of variation for 10 replicates on 3 samples of different levels of phosphorus in μg/litre

	a	*b*	*c*
Mean of 10 samples ..	1·14	6·61	158·4
S.D.	0·8124	1·7433	4·0552
C.V.	71·26%	26·37 %	2·56 %

Thus the error of the instrument is seen to be high, when expressed as a coefficient of va but not so high when expressed in μg/litre. (Harvey, 1948, expressed the error of his abs meter, a very much superior instrument, as ±0·25 μg/litre.) There are two types of error, h that lie outside this estimate; (*a*) it is possible that the overall operational error at sea is consi greater; (*b*) one point of making an average of the four levels near the surface, is to red overall error by half; it is possible that this procedure is not permissible. Both these probl tackled by the use of an analysis of variance, using Stations as rows and Depths as col see Table XV.

Table XV

Analysis of variance of observations of phosphorus in μg/litre; Cruise VI, Sir Lancelot, 1949

	DF	*MSq*
Stations	29	37·684
Depths	3	36·230
Interaction	87	12·541

The Main Effect " Depths " is not significant, so it was pooled with the Interaction t residual Mean Square of 13·331 from which a standard deviation of 3·651 is calculated. this value, the coefficient of variation of the mean is 35·82 per cent. Examination of the n the values at each depth shows that there is a tendency for values to increase with dep theoretically correct effect has not yet had time to appear strongly, for the turbulent sea not quite finished, so the Main Effect " Depths " is not significant. Thus the coefficient of v from the analysis may be used to express an overall error of 35·82 per cent, which is to be e from a mean value of about 10 μg-litre. As there were four observations for each Mean Phosphorus value, its variance will be $\frac{1}{4}$ of that of a single observation. This reduces the c of variation on the Mean Surface Phosphorus values to 17·91 per cent (i.e., about $1\frac{1}{2}$ μg/litr

(iii) *Phosphorus distributions.* The Mean Surface Phosphorus values in Figs. 6 and 7 toured at 0·1, 0·2, 0·3, 0·4 μg-atoms P/litre. Fig. 6 shows the distribution in Cruise VI, Sir L 1949, and Fig. 7 shows that in Cruise VII, Sir Lancelot, 1949. Taking the central date cruise, Cruise VII occurred 13 days after Cruise VI. Two observations may be made charts.

(1). The central area of low phosphorus values occurring both in Fig. 6 and Fig. correspond with the diatom patches in Fig. 5.

(2). The phosphorus uptake between the two cruises was 2·35 μg/litre or 0·073 μg-at Consequently the contour at 0·30 μg-atoms/litre in Cruise VI (Fig. 6) is roughly compar that at 0·20 μg-atoms/litre in Cruise VII (Fig. 7). It appears that the whole system ha slightly to the south.

3. Patches of Plankton Animals

Copepods, the main herbivores and, at the same time, the main food of the herring, were i as nauplii, copepodite stages I–V, ♂ and ♀ of *Calanus finmarchicus*, ♂, ♀ and juv *Paracalanus parvus* Claus, ♂, ♀ and juveniles of *Pseudocalanus elongatus*, and *Temora lo* The patches of these stages, sexes and species were contoured by the method described ir in this section only the *Calanus* patches are considered, because it is in the distributio copepodite stages I–III of *Calanus* that the identity of the groups of patches is maintained cruises. Figs. 8 and 9 show the distribution of *Calanus stage V* in Cruise VI, Sir Lancel and *Calanus V* in Cruise VII, Sir Lancelot, 1949; these examples were taken at random to the consistency of the contour systems. In this they resemble the plant systems of Fi here also, each observation confirms the whole system; it is not the case that merely o observations are used to mark a peak. Thus the highest contour level or peak level, a may surround but one observation, is itself supported by many more.

. 10 shows the groups of *Calanus* patches of each copepodite stage on each of the five cruises; patch is represented by the highest contour level, for the sake of simplicity. If the full evidence ch patch were presented, the pictures would be so complex that they would be meaningless, ch picture is of the type shown in Figs. 8 and 9. In general, however, the highest contour level represent the shape of the patch. The conclusion that may be drawn from Fig. 10 is that atches of *Calanus* copepodite stages exist in groups and that each group is a separate entity. roups cover extensive areas, but there are marked and consistent gaps between them. The groups, indicated by letters in Fig. 10, are separated in this figure by arbitrary lines drawn gaps between the groups. The problem is to find the identity of these groups of patches from to cruise; there are a number of possible identities that may be made. We already know the phosphorus distributions that if there was movement between Cruise VI and Cruise VII, a slight one to the south; this is not a reliable method and becomes less so as the season

DISTRIBUTION OF *Calanus*, STAGE V

G. 8. CRUISE VI, SIR LANCELOT, 1949
Stations are as in Fig. 10.

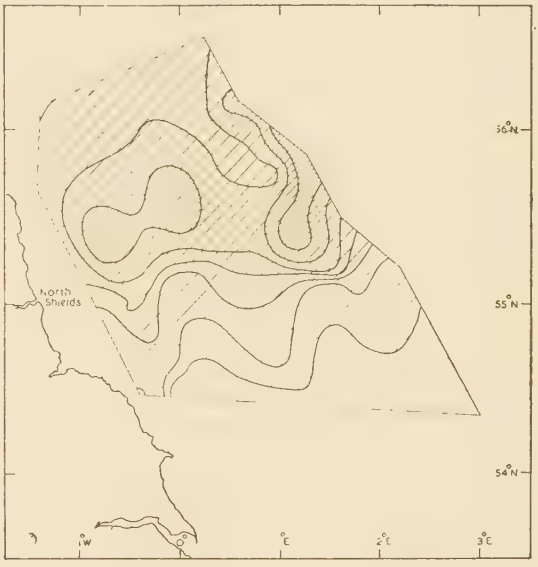
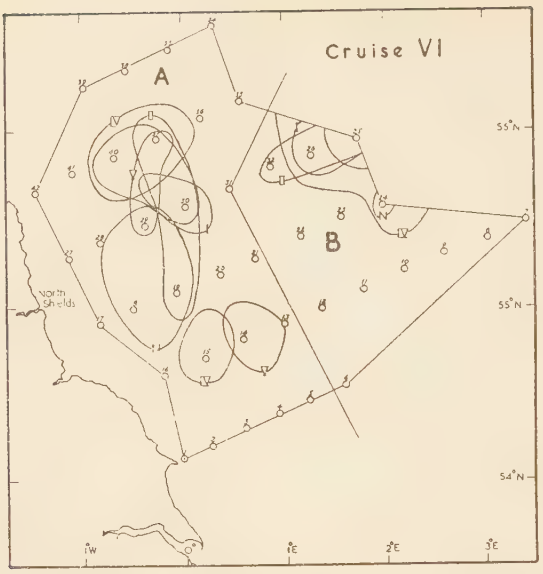
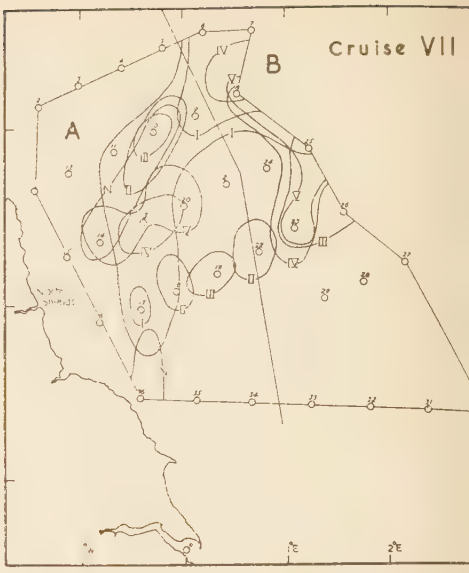


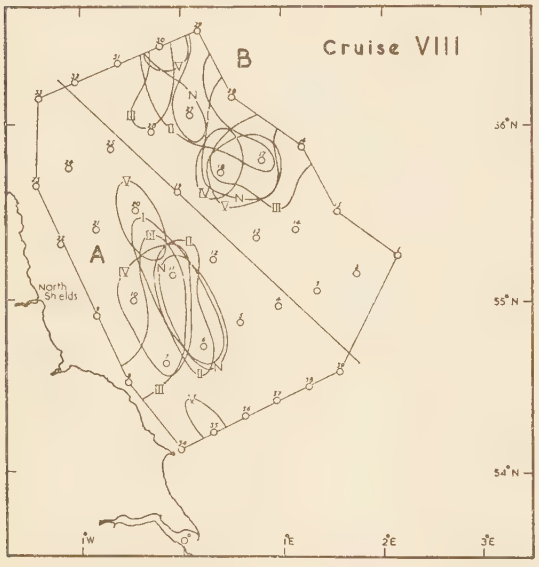
FIG. 9. CRUISE VII, SIR LANCELOT, 1949
Stations are as in Fig. 10.

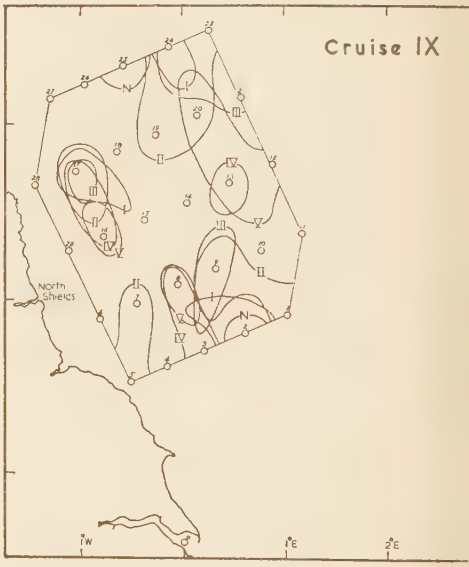
ces because there is not a steady uptake of phosphorus with time and during the later s there is possibly a regeneration of phosphorus. Hydrographic information is in support general southward movement, but the rate of the drift and its detailed directions are own.

e arrangement of the patches within a particular group can be connected in the age order of opepodite stages; e.g., I–II–III–IV–V, to make a consistent pattern on a chart. It might be ght that this was a summary of the recent history of the water movements, and most neat legant patterns are often the result. Such patterns would be useful indices of the water move- s if the spawning ground was always " upstream " of the patch of copepodite stage I; as it be " downstream " of the patch of copepodite stage V, the argument and the pattern become ar—unless a marked invasion takes place. In view of the relation between egg production eeding (Marshall and Orr, 1952), spawning is probably randomly placed across the direction w of the main current, because of the local distribution of phytoplankton. Thus each patch y pattern could have originated from a different position relative to the direction of flow of ain current.









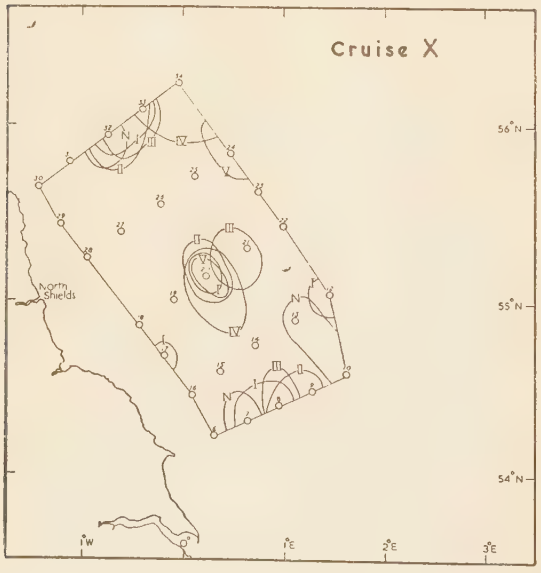


FIG. 10. GROUPS OF PATCHES OF *Ca*
STAGES OFF THE NORTH-EAST COAST IN

Each outline represents the highest contour le
a given copepodite stage; the number of the s
inset in the outline, in Roman numerals. Stati
represented as open circles; the station numb
shown alongside. In Cruises VI-VIII, each gr
patches is indicated by a letter.

distinguish the patch groups from one another, it was decided to measure the sizes of animals :h. Distributions of *Calanus* measurements are polymodal (Adler and Jespersen, 1920; ll, 1928; Marshall, 1933); yet, it is quite clear from the trend with time of the medians of these rements (Russell, 1928; Marshall, 1933) that there is a decline in size during the early summer, he diatom outburst. It was thought that analysis of such polymodal populations during ı size decline might reveal differences that could be used to identify the patch groups from to cruise. It was with the use of such size differences that Baldi *et al.* (1945) first established fferences between populations both horizontally and vertically. To apply the method here, necessary to decide which copepodite stages to measure. As *Calanus* " *helgolandicus* " is vhat larger than *Calanus finmarchicus*, it was also necessary to consider the distribution of o forms.

Calanus " *helgolandicus* ". Preliminary measurements showed that there appeared to be a form of the copepodite stage V's in the northern part of the area and it was thought that might be *Calanus* " *helgolandicus* " (Rees, 1949). So, at each station on Cruise VI, Sir :LOT, 1949, 50 animals were identified as copepodite stage IV, V and females of *Calanus chicus* or " *helgolandicus* ". Fig. 11 shows the distribution of percentages of *Calanus*

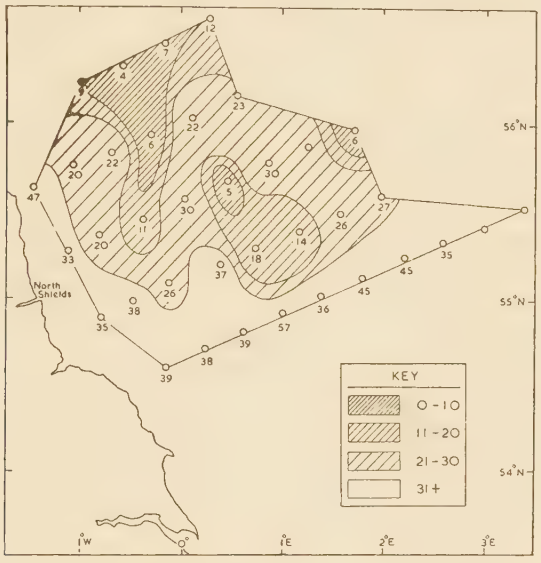


FIG. 11. *Calanus* " *helgolandicus* " EXPRESSED AS A PERCENTAGE OF TOTAL *Calanus* AT EACH STATION

Calanus " *helgolandicus* " is identified as stages IV, V and ♀, so only these stages are included in the estimate of total *Calanus*. Contours are drawn by eye. The dark shading is, in fact, a distribution of *Calanus finmarchicus*.

landicus ". The percentages are low in the northern area, so the northern large form in and Fig. 10 appears to have been in fact *Calanus finmarchicus*. However, in the south, a) half of the population consisted of *Calanus* " *helgolandicus* ". So it was decided to extend ntifications to all cruises.

same type of distribution of percentages of *Calanus finmarchicus* was shown for the areas of ." groups of patches in Cruises VII and VIII. An analysis by stages in Table XVI shows ere is a change in the percentage recruitment of " *helgolandicus* " into the copepodite stage IV. oportion of " *helgolandicus* " gradually increases during April and May.

Table XVI

Proportions of *Calanus* " *helgolandicus* " in the " A " group of patches during Cruises VI, VII, VIII, Sir Lancelot, 1949

	Stage IV		Stage V	
	Finmarchicus	" *Helgolandicus* "	*Finmarchicus*	" *Helgolan*
Cruise VI	149	14	138	23
(Sta.: 29, 30, 31, 35, 36, 37, 38, 39, 40)		9%		14
Cruise VII	83	15	67	3
(Sta.: 13, 19, 20)		15%		4
Cruise VIII	95	26	74	23
(Sta.: 6, 7, 10, 11) ..		21%		24

As the " A " group of patches move south, it changes its character, from being composed completely of *Calanus finmarchicus* to being about three-quarters composed of *Calanus finma* This may be interpreted in two ways: (1) *finmarchicus* suffers in competition with " *helgolan* (2) " *helgolandicus* " is derived from *finmarchicus*. If the two types do not interbreed, the study of the *Calanus* populations they would have to be separated. As the stocks are ob and inextricably mixed in space, and as the anatomical difference is small, it is possible th could interbreed. There is a strong case for treating the two types as one for population a there is no evidence of inter-type sterility, there is no separation of breeding in time or sp the naupliar and copepodite stages cannot yet be distinguished until sexual maturity starts to This latter point means that if the two types were separate, an age distribution (in terms of dite stages) cannot be made. The use of such an age distribution is to estimate the mor *Calanus* due to grazing by herring. For the limited purpose of estimating how many c the herring consume, it is worth while considering the population as one interbreeding possible. As the status of *Calanus* " *helgolandicus* " is not yet decided and as we do n whether the two groups do or do not interbreed, the populations will be considered as one tion of " *Calanus* ".

The copepodite stages of *Calanus* used to make the identity of " A " group of were stages I–III; one reason for choosing these smaller stages was to avoid the size dif in stages IV, V and ♀ between the two types of *Calanus*. But it might be possible " *helgolandicus* "-*finmarchicus* size difference might also appear in the smaller stages. animals that were separated were also measured; work was carried out for me by Mr. H Woodhead. The results are shown in Tables XVII and XVIII; it is clear that there is v difference, in size, if any, between the two forms in the copepodite stage IV, but there is a difference in the copepodite stage V, and a marked difference between the females. Thi sistent with Rees' observations, but our differences were not so marked as his. Thus it is that differences in size observable in the copepodite stages I-III are not due to the separati two forms, because this does not seem to appear until the onset of sexual maturity.

Table XVII

Mean sizes of *Calanus* (mm.) within the " A " group of patches. (Suffices indicate the number of observations)

		Finmarchicus			" *Helgolandicus* "		
		IV	V	♀	IV	V	♀
Cruise	VI	$2{\cdot}4611_{167}$	$3{\cdot}1093_{90}$	$3{\cdot}5709_{32}$	$2{\cdot}4338_{31}$	$3{\cdot}1417_{12}$	3·5
,,	VII	$2{\cdot}4033_{86}$	$3{\cdot}1278_{57}$		$2{\cdot}3553_{15}$	$3{\cdot}3540_{2}$	
,,	VIII	$2{\cdot}3448_{83}$	$3{\cdot}0196_{50}$	$3{\cdot}3072_{10}$	$2{\cdot}3468_{23}$	$2{\cdot}9341_{27}$	

Table XVIII

Mean sizes of *Calanus* (mm.) for all stations of all cruises

		Finmarchicus			" *Helgolandicus* "		
		IV	V	♀	IV	V	♀
Cruise	VI	2·4417	3·0807	3·5617	2·4073	3·1066	3·5
,,	VII	2·4054	3·0800	3·5070	2·3995	3·2349	3·6
,,	VIII	2·3067	2·9252	3·4112	2·3611	2·9756	3·7
,,	IX	2·1755	2·7895	3·3243	2·2200	2·7807	3·4
,,	X	2·0900	2·7371	3·1005	2·1320	2·7722	3·1

uring this work, Mr. Woodhead made an attempt to separate the copepodite stage V's of
i forms into ♂ and ♀; a separation was achieved for *finmarchicus*, but in a sample of 159 stage V's,
as unable to find a male " *helgolandicus* ". He found that the three groups ♂ and ♀ *finmarchicus*
♀ " *helgolandicus* " could be distinguished by the degree of curvature on the first abdominal
nent. The *finmarchicus* ♂ was not curved, the *finmarchicus* ♀ was markedly curved and the
helgolandicus " was very markedly curved. These results are shown in Table XIX.

Table XIX

Separation into the sexes of stage V *Calanus*

		Finmarchicus		" *Helgolandicus* "	
		♀	♂	♀	♂
Cruise	VIII Sta. 8 ..	13	16	10	—
,,	IX ,, 6 ..	33	8	5	—
,,	,, ,, 16 ..	11	4	5	—
,,	X ,, 12 ..	10	2	14	—
,,	,, ,, 15 ..	21	7	10	—

he method was not completely satisfactory because four out of 88 *finmarchicus* male approached
" *helgolandicus* " female condition. Two out of 44 " *helgolandicus* " female approached the
archicus female condition. On the other hand, in four of the " *helgolandicus* " the curve
roached that of a mature ♀. The investigation of sizes did not disturb the decision to treat
" *Calanus* " population as one and that it seems unlikely that any size differences found in
es I–III are due to the presence of *Calanus* " *helgolandicus* ".

i) *The polymodal populations of copepodite stages I–III of* " *Calanus* ". Three possible reasons
be suggested for polymodality in copepodite stages V:

i) that there is a difference in size corresponding to a sex difference;

i) that there is a " growth factor " difference. Sewell (1932) used this term to show that a particular stage was so many times larger (this is the growth factor) than the preceding stage, particularly in the older stages;

) that there is a difference in size between *Calanus finmarchicus* and *Calanus* " *helgolandicus* ".

hese types of difference cannot easily be detected in the copepodite stages I–III. Bogorov
4) wrote that the size measurements of stages I, II and III were unimodal, so these were used
this purpose. However, in the present material, these stages showed a polymodality of some
in different from that in stage V; fifty specimens of each of the three stages I, II and III were
sured at each station of each cruise of Sir Lancelot, 1949; measurements from various stations
e combined to give distributions showing the character of the patch groups. The resulting
ibutions were thus made of 100–200 measurements on each stage. Fig. 12 shows that these
bined distributions were polymodal; this polymodality was not the result of combination,
ough mixed distributions could be made in this way. Each station was examined separately
found to contain the basic polymodality of the patch group.

ig. 12 shows the frequency distributions for each copepodite stage and each cruise arranged
g a scale of length. Thus each set of three stages can be compared with another by noting its
tion on the scale relative to the set above or below. It is immediately clear that the copepodite
es I–III in the " A " group of patches are consistently larger than those in the " B " group.
ain each group the sizes of each of the three stages remain consistently the same for the three
ses. Thus it is reasonable to assume that the " A " group in Cruises VI–VIII is in fact the
e group; this might also be said of the " B " group, but this is not completely sampled. If the
tification in the " A " group is true then it can be seen from Fig. 10 that the " A " group of
hes has drifted in to the area from the north-east and has drifted out past Whitby before
se IX was started.

'e may sum up the evidence for the identity of the " A " group of patches during the first three
ses of the series. As these groups were completely delineated in the grid of stations, we may
that they were completely sampled and that they are identical populations. The line between
h groups is necessarily arbitrary, but there is clearly a significant size difference between the
groups of patches, that cannot be attributed to sex difference, the difference between *Calanus*
archicus and *Calanus* " *helgolandicus* " or to differences between possible growth factors,
hese characters only appear in the maturing copepodite stages.

There are two sets of patch groups in Cruises VI, VII and VIII; these are distinguished b difference that is consistent and of the same order through the three cruises. The consequ this size difference between the two groups of patches is that the " A " group of patches is id from cruise to cruise as being the same patch. In view of the decline of size shown by Russel and Marshall (1933) a remarkable point is that the stage I's continue to be produced of th sizes in the two sets of patches through these three cruises.

(iii) *Size of copepods.* Decrease of median size of copepods in the early summer has bee buted to a number of factors. Adler and Jespersen (1920) show a relation between large s low temperature; Störmer (1929), Jespersen (1939), Bogorov (1934), and Deevey (1948) measurements from a wide variety of areas, came to the same conclusion. Clarke and Zinn however, related large size and high temperature, but this was because one of the two broo was an overwintering generation. Confirmation of the earlier thesis experimentally, was

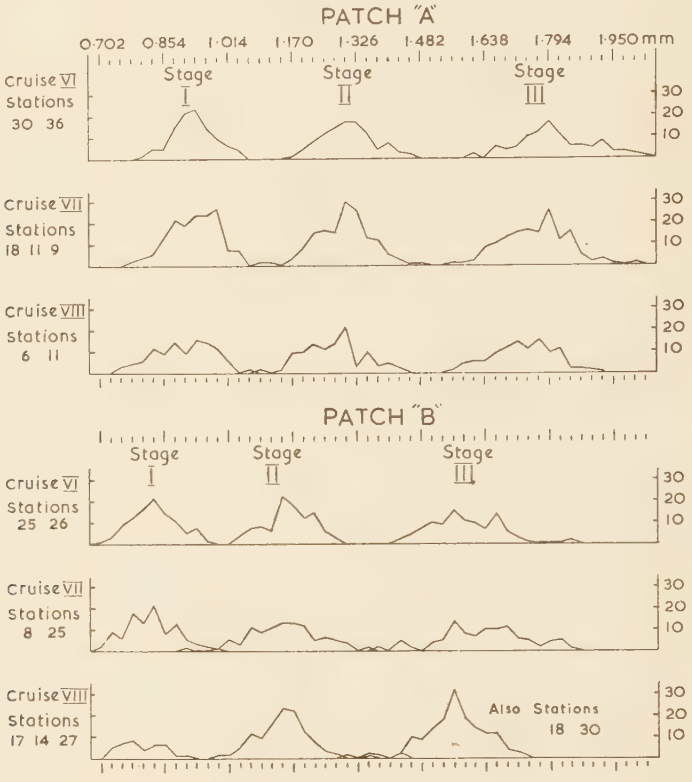


FIG. 12. *Calanus* SIZES, OF STAGES I-III, FROM PATCH GROUPS " A " AND " B "
Cruises VI–VIII only are used.

out by Coker (1933) who reared *Cyclops vernalis* Fischer at different temperatures under c food conditions and found that the larger animals were reared at lower temperatures. Ussin has suggested that the different sizes depend on the relative availability of food in differen Raymont and Gross (1942) have shown that the survival of copepodite stage V's thro moult depends on the food concentration in the cultures that they used.

However, Marshall (1933) wrote that water temperatures cannot have been responsible variations through the summer and that diatom concentrations bear no relation to size distri The same conclusion may be drawn from Wimpenny's results (1933) on *Calanus finmarchic* Flamborough area. This raises the question that another factor may be involved. Co Miss Marshall's results for 1933, 1934 and 1949, for numerous species of copepods, it appe the maximum size is reached in April, the time of the spring increase; subsequently the food of the water decreases and the temperature increases. Russell (1928) showed that differen live at different depths, and Marshall (1933) showed that there was a depth gradient in larger animals living at the greater depths; Gardiner (1931) noticed that the small *Cala*

er the surface. Although there is no evidence for it, it is possible, as has been suggested earlier, the polymodal populations within stages shown in Fig. 12 are a depth series, which of course d not appear in a vertical net sample. It is interesting that a few of Rees' (1949) curves of distributions are unimodal; these were taken from 10 m. Sewell (1948) suggests that there be different forms of various copepods—dwarf and giant forms; Jespersen (1928) showed *Calanus finmarchicus* in E. and W. Greenland had two forms that were distinct in size urements.

ıe observations recorded in this short review of some of the literature suggest that what happens follows. There is a decline in median size in the early summer after the spring increase that is rently related inversely to temperature. There seems to be no such decline within a particular d, the change being effected possibly by the extinction of the brood and by its replacement naller animals. Presumably the constant recruitment of stage I's of constant size is due to the that the females of this brood are still breeding. Bogorov (1934) suggests that the size attained ıe adult is a function of temperature. Whether or not this is so when food is also decreasing ıantity, it remains that the change of size should occur fairly sharply, when the smaller adults to reproduce.

sum up, size measurements of copepodite stages I–III of *Calanus* have been made from the ent groups of patches. The distributions of measurements were polymodal, being composed o or three component populations. It is thought that the decline in median size during the summer is due to the replacement of the larger component populations by smaller ones. is assumed to depend on the length of the breeding stage of the adult females (assuming that les of the same size produce offspring that remain consistently in the same size group) and on onmental conditions within each group of patches. It is the degree of difference that makes dentity between cruises convincing.

URATION OF COPEPODITE STAGES

fore the numbers of each copepodite stage may be used to make an age distribution that can mpared from cruise to cruise, it is necessary to consider the duration of the copepodite stages. ıking a central date for each cruise, the time intervals between cruises are as follows:

Table XX

Time intervals between cruises (in days)

	VI	VII	VIII	IX	X
Cruise	13	18	13	15	

e number of moults can be assigned to these time periods, age distributions of *Calanus* for the ified patches for each cruise can be made. There is a disagreement in the literature between esults of laboratory experiment and the results of field observations. On the one hand Nicholls) cultured *Calanus* and came to the conclusion that the minimum interval for each copepodite was three days and that 28 days cover the time from egg to adult. On the other hand, Ruud), Fish (1936) and Rees (1949) suggest that the total development time from egg to adult is 70–90 days. Nicholls' field observations (1933) were interpreted to show that one copepodite lasted about 5–7 days; his diagrams show that all copepodite stages appear initially together, ing that an invasion had taken place.

e difficulty may be resolved in the following way. The field observations taken by Ruud, and Rees, were taken at comparatively low temperatures, whereas Nicholls' experiments were at 14°–15° C. (personal communication from Dr. S. M. Marshall) and in the present vations the sea temperatures started at about 6° C. For the duration of physiological processes temperature, Belehrâdek used the following formula: $y = \frac{a}{b^t}$, where y is the duration, t is the erature and a and b are constants. This has the advantage over the Q_{10} formula in that the on is linear over all its range. From the type of result given by Belehrâdek (1935) one would t that a duration at 6° C. would be expanded by $2\frac{1}{2}$ to 3 times that at 15° C. Dr. Marshall has y allowed me to see Nicholls' original results. The mean moulting time for stages I–II and was three days and that for the older stages was seven days. The durations multiplied by times give $7\frac{1}{2}$–9 days for the small stages and 17–21 days for the large stages. Thus between resent cruises, the nauplii might have moulted not only to copepodite stage I, but also to

stage II; this quite possibly did occur. Beyond this, one stage per cruise seems to be a reas estimate, because temperatures were slowly rising from 6° C. to 9° C. during the cruise serie age distributions of *Calanus* can be made, assuming that each copepodite stage moults b each cruise. Shorter and longer time intervals were also tried, and they resulted in compl meaningless pictures. Although there seems no objection to the assumption made, the q can only be finally resolved by experiments on the breeding of *Calanus* at different temperat

4. Age Distributions of *Calanus Finmarchicus*

Using the numbers of each copepodite stage from the " A " group of patches from each and assuming that each stage moults between cruises, three age distributions were made. are shown in Fig. 13. The histograms have been plotted in two ways; (*a*) with the cope

AGE DISTRIBUTIONS FOR *Calanus* COPEPODITE STAGES

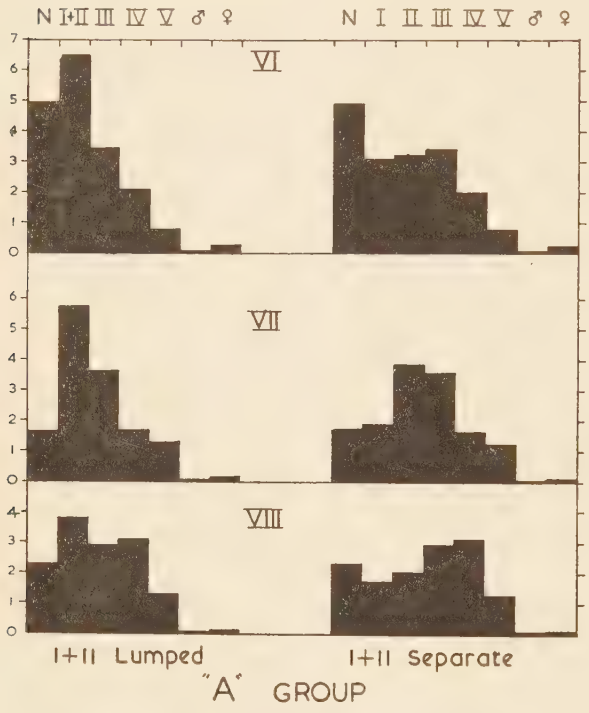


FIG. 13.

Each column in the histogram represents an estimated number × 6·4 × 10^{13}; the " A " group of patches was used as a basis for this estimate. *Calanus finmarchicus* and *C.* " *helgolandicus* " are included together in the estimate.

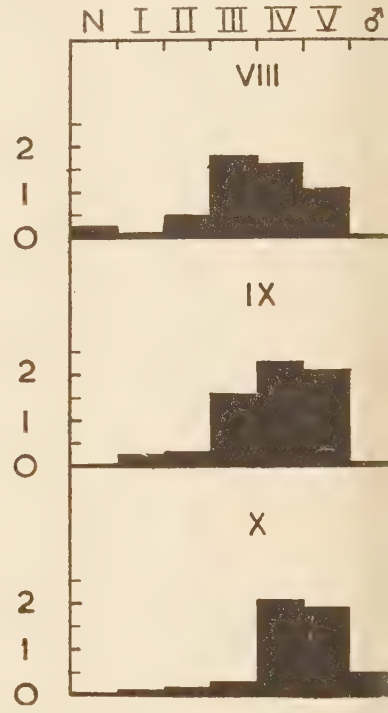


FIG. 14.

Each column in the histogram rep an estimated number × 6·4 × patch groups in Cruises VIII–X used as a basis for this estimate. *finmarchicus* and *C.* " *helgolandic* included together in this estim

stages I and II lumped; (*b*) with these stages separated. It is possible that the former is th appropriate. The latter, however, shows that the nauplii, stage I and stage II in cruise V well become the stage II and stage III in Cruise VII and that these, in their turn, could well the stage III and stage IV in Cruise VIII. It may be noted in passing that this is slender ad evidence in favour of the identity of the " A " group of patches.

The age histograms from Cruises VIII–X (Fig. 14) are not taken from groups of patches ic in the same way as the " A " group. It is possible to argue that these groups are the same are shown, however, in order to compare them with the " A " group.

Taking all the age distributions, the following points can be made. There is a sharp de the number of nauplii in Cruises VI–VIII in the " A " group; this makes for a reduced recru In Cruises VIII-X in a different group of patches, the recruitment is reduced to insig

ortions. The second point is that there is very little mortality on the nauplii, stages I and II, nat the older stages suffer very heavy mortality—particularly the stage V. Thus the number of s is very small indeed. The third point is that the number of adults increases very sharply in e X.

er a longer period, this type of method would show whether the loss of recruitment was due ck of plant food or to the reduction of numbers of adults, whether the heavy mortality in the stages was due to grazing by the herring or was due to a " natural " mortality, and lastly her the increase in the numbers of adults in Cruise X was related significantly to a decrease in umber of herring. Such a decrease did occur, as will be shown in Part IV. On such a small ber of observations it is impossible to do more than speculate.

5. The Movements of the Groups of Patches

is accepted that the " A " group of patches has moved southward during Cruises VI–VIII, if it is also accepted that the copepodite stages moult between cruises, then the movement of patch may be traced from cruise to cruise. Thus the centre of a patch of copepodite stage III ruise VI may be connected by a line drawn on a chart to the centre of a patch of copepodite IV in Cruise VII, and in turn, the centre of this patch of copepodite stage IV may be con- d to the centre of a patch of copepodite stage V in Cruise VIII. For this purpose, the groups itches must be identified from cruise to cruise, for it would be meaningless to connect patches different groups.

iis procedure has been carried out and is shown in Fig. 15. Each chart is marked with a number nes, each of which is the connecting line between patches, i.e., the line of movement of the h. Thus each chart shows the possible movements of each patch between cruises. The first charts are concerned only with the patches in or replacing the " A " group. The chart of ement between Cruise VI and VII is concerned only with the " A " group, except for three iingly invading patches that come in from the north-east and two patches that drift out to the h. It is the southward movement of the identified " A " group that allows it to be inferred that north-eastern patches are invaders and that the two southern patches in Cruise VI have moved h out of the area in Cruise VII. It is the same southward movement of the identified " A " h that allows it to be inferred that the invaders from the north-east in Cruise VII have moved more central region N.E. of Shields in Cruise VIII. Similarly the two southern patches in se VII are considered to have moved further south and out of the area.

uring the subsequent cruises the only identified group of patches, the " A " group, moves out ie south. Also the group that replaced the " A " group has moved out. The interpretation of remaining movements is the simplest that can be made, assuming a southward movement. s the invading patches in Cruise VIII are assumed to be of two groups that move south-westward Cruise IX; the only other way to interpret this would require that the two groups cross each r, the one moving south and the other moving west. A local swirl could effect this, but there evidence for it. Between Cruises IX and X, the two groups of patches are assumed to move hwards and there is a further group of invaders from the north-east.

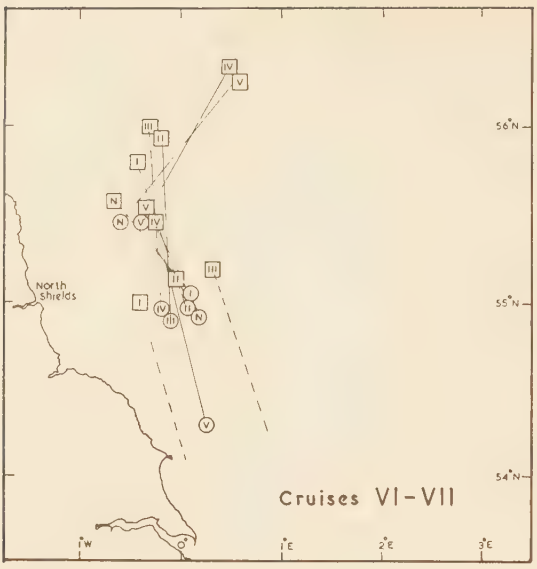
is realized that this interpretation of the movements of patches between Cruises VIII and X ghly speculative. Although I have argued that groups of plankton patches can be identified cruise to cruise, this was not carried out on these patches because the numbers of stages I–III *alanus finmarchicus* were very small. The justification of the interpretation is that it illuminates possibilities of the method—for it is difficult to find how a water mass with its compresent kton has moved over a short period.

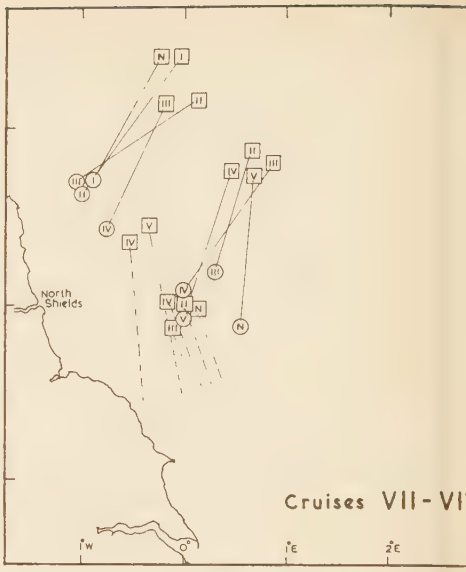
he travel lines of the patches on the chart may be used to find the speed at which the patch has elled between cruises. As a number of patches were used, it is possible to estimate the mean d of patches in miles/day. This is shown in Table XXI.

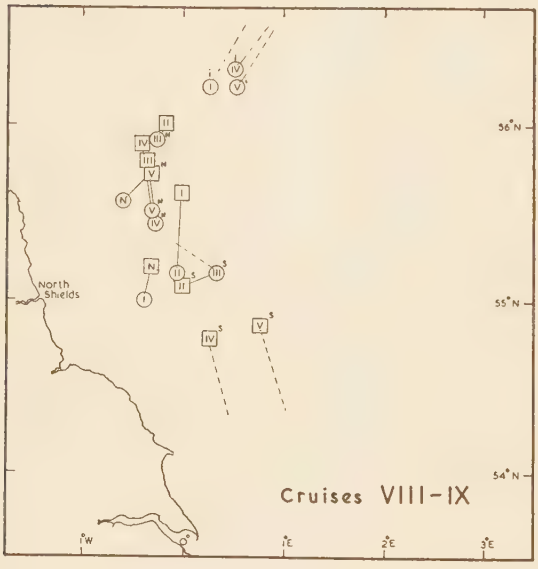
Table XXI

Mean speeds of patches between cruises (in miles/day)

Cruise VI–VII	VII–VIII	VIII–IX	IX–X
0·98	3·13	3·52	2·51







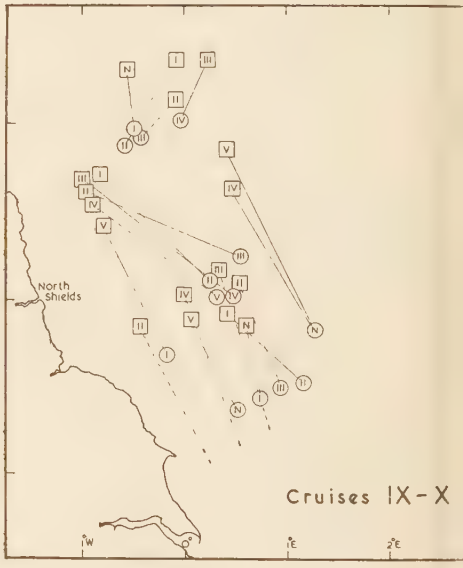


FIG. 15. MOVEMENT OF PATCHES BETWEEN CRUISES

□ indicates the patch of a given copepodite stage on the first cruise.
○ indicates the patch of the succeeding copepodite stage on the next cruise.
Suffices: N—northern; S—southern; I—invading.

The first two estimates are made from the movements of the identified " A " group of pat the assumption that the copepodite stages moult between cruises, which has been sh unreasonable. The second two estimates are not so firmly based, but they are consistent first. Apart from suggesting that the water masses increased their speed during the per then possibly decreased it, no hydrographical interpretation will be attempted.

The relation of plankton organisms to their hydrographical background is often writte word " indicator ". There are a number of meanings to this word (*a*) the physical or c limit to an animal's distribution " indicates " a physical quantity, e.g., *Limnocalanus* g de Guerne is limited in horizontal distribution by a particular value of salinity and is alsc in vertical distribution by a particular value of temperature (Ekman, 1935). Thus one c the distribution of this animal to find this value of salinity and this value of temperature.

of a water mass may restrict an animal's distribution, merely because there is no mixture across oundary. Thus, sailors recognize the Gulf stream and the Humboldt current by the presence e whales and birds that feed on the plankton confined in these streams. Similarly one could ie distribution of some plankton organisms to find the position of such a current; this would ork in a mixing area or in the diffuse drift that is the latter end of such a current. (*c*) The irance of invaders or exotics marks the presence of a water mass from a distant region. The bution of invaders can throw some light on the origin of a water mass, but none on its time of irance. (*d*) A water mass is indicated by a community, of which a long-lived predator becomes indicator ".

e intention of work on " indicator " organisms is to throw light on the distribution and ments of water masses, additional to what can be done hydrographically. The present work a new meaning to the word " indicator ". If the groups of patches of plankton animals can entified from cruise to cruise, then details of the speed and direction of water masses can be lated. Other forms of indication cannot do this.

6. Summary

and animal patches were contoured as described in Part II and their numbers were estimated. osphorus distributions were described and the errors in method estimated. The relation en plants and phosphorus is described and it is suggested that destructive grazing of the plants ot yet taken place in April 1949. The phosphorus distributions themselves were used to show thward drift in the area.

s of animals were measured in each of the groups of patches. The consistent size difference (that was not attributable to the presence of *Calanus* " *helgolandicus* ") between two groups, g three cruises, was considered to make highly probable the identity of one particular patch g the three cruises.

vas assumed that the copepodite stages of *Calanus* moulted between cruises. This is not sonable; from this assumption, an age distribution of *Calanus* was made and an attempt was to estimate the speeds and directions of movement of the patches. This is the essential step cidating the dynamic cycle. Until patches can be identified, by one means or another from to cruise, there is no point in trying to establish the relations between populations within atch. It is no accident that the zooplankton have been used to make the patch identity, for anges in numbers of the zooplankton lie at the very centre of the dynamic cycle. The numbers plants change due to grazing by the animals; the numbers of aggregating fish change as the ers of plankton animals change. Thus the meaning of the word " patch " is taken at the nkton level; for patches of pelagic fish and phytoplankton owe their existence and their to the working of the dynamic cycle that is centred on the plankton animals.

Part IV

The Relation between the Herbivorous Zooplankton and the Pelagic F

1. Introduction

The relation between *Calanus* and the herring has been discussed many times; the lite reviewed in Part I. The methods used here have already been described (Cushing, 1953) and Table XXII have already been published. They are reproduced here because it is fel examination in greater detail would be profitable. Again, Fig. 24 has already been publis Figs. 25 and 26, which illuminate the drifter-herring relation to a greater extent, have published. The method of echo survey (Cushing, 1952) has been reconsidered here in son partly because a number of surveys of different character have been carried out since t partly because my understanding of underwater acoustics has improved since the paper m above was written.

The aggregation of herring on to the *Calanus* patches is measured with the use of the co coefficient. A transfer of aggregation from stage V to stage IV is shown to take pla *Calanus*-herring relation is finally described in terms of three balancing factors, the repr rate of *Calanus*, the death-rate of *Calanus* and the aggregation and disengagement of the The reproduction and mortality of *Calanus*, if they can be determined and understoo provide knowledge of a great part of the dynamic cycle, because the reproduction rate o is probably dependent upon the rate of plant production, and it is also probable that the death-rate is dependent upon the change of numbers of pelagic fish.

2. Use of Echo Survey to Estimate the Abundance of Herring

One requirement for the study of the *Calanus*-herring relation is a proper estimate of the of the fish. The abundance of herring was, however, difficult to estimate because the dri to work within only 30 miles of the coast, whereas the cruise grid (designed to circum *Calanus* patches), extended seaward for 120 miles. Thus, fish samples caught by drift represent the fish distribution over only a small part of the area. The difficulty was a estimating indices of fish abundance with a form of echo survey. This method has been in Cushing (1952).

In summary, the method is as follows. The echo sounder was run continuously be plankton stations, and the paper records were preserved. Fish traces on the paper re measured in width microscopically. Soundings that succeed each other on the paper most commercial echo sounders become superimposed; if the degree of overlap between is known, it is possible to convert the width of a trace into the number of soundings. fish traces, the number of soundings on fish were added together along the paper rec between stations, and were assigned to " echo stations " midway between the plankto When these numbers were plotted on the cruise chart, they were combined by contouring the probable areas of abundance of pelagic fish. This method has been tested on the di of herring shoals off East Anglia and on the distribution of pilchards in the English Ch may be noted that distribution of herring landings from drifters off East Anglia and the di of pilchard eggs in the English Channel provided a general means of identification (Cushi but no identification of individual shoals was made.

Krefft and Schüler (1951) have described another method of survey. They make depth of the trace and its extent in depth, to make an index of abundance within each It must be remembered, however, that the amplitude of a returned signal is subject to a variables: (1) the position of the fish shoal relative to the axis of the sound beam is

ere might be confusion between a signal from a small number of fish on the axis and a large r at the edge of the beam, so it is difficult to assign a number of fish to a particular fish (2) power output and amplifier gain on commercial sounders are variable, particularly when n fishing vessels, the mains voltage of which are not always kept steady; (3) any returned must be measured as referring to a level of noise; the factors determining this level from day are largely unknown and are often capricious. It is thus unlikely at the moment that a estimate of the numbers of fish within one recorded fish shoal can be made. The advantage method used in the North Shields series of cruises is that it is really based on the presence or e of fish within a particular sounding, and that it implies nothing about the relation between rs of fish and the returned signal amplitude.

e 1949, a number of echo surveys have been made in which each trace has been identified agnostic character. One set was carried out on the winter sprat shoals of the Southern Bight s successfully shown a new area for sprats off Ijmuiden (Richardson, 1950, 1951). Another was carried out on the summer herring fisheries off Fraserburgh and a significant correlation tained with drifter landings, making a " general identification " that the fish were herring h and Craig, 1951). If identification of each trace is made, then the estimates of abundance clude individuals of other fish species that make the same sort of trace; conversely, such cation will exclude the desired fish species when it makes traces that are different in character, xample, due to a change in behaviour. If identification of each trace is not made, the estimate ndance will include all pelagic fish; in this case, this is preferable, because all the pelagic fish, ed in this way, are likely to be *Calanus* feeders.

3. Relation between the Echo Survey and the *Calanus* Distributions

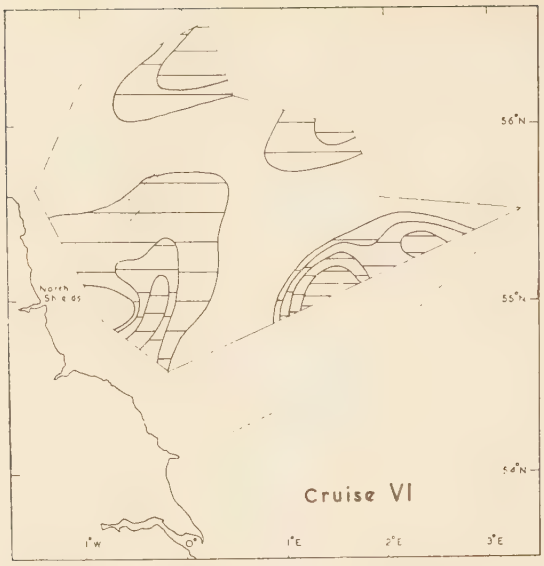
ho survey and the *Calanus* survey cover the same area at the same time. The discussion of lting distributions is in two parts (*a*) the pictorial representation and (*b*) the use of correlation ents as a measure of aggregation.

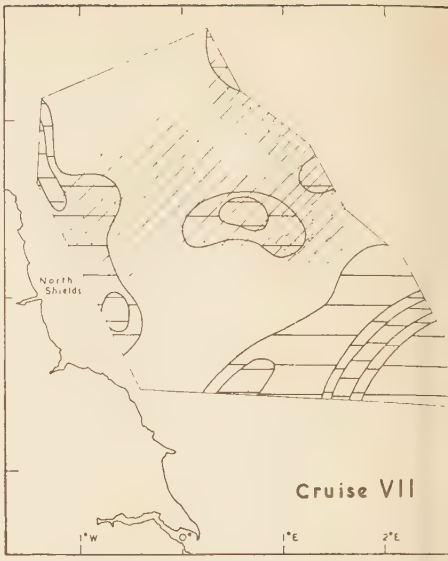
TORIAL REPRESENTATION

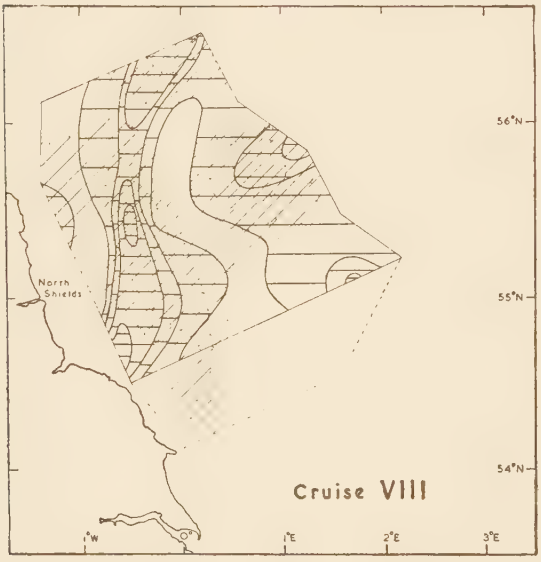
16 is a pictorial representation of the echo patches and the patches of *Calanus* stage V, 1 of the five cruises VI–X, Sir Lancelot, 1949. The echo patches are shown completely and every observation, but the *Calanus* patches are shown only at the higher levels contoured. to simplify the representation. As the lower contour levels follow the conformation of the ones, little information is lost in this way.

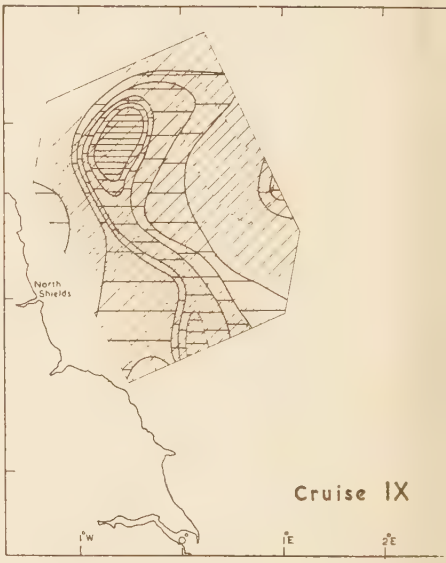
ruise VI there is no relation between the two distributions; neither is there any relation n them in Cruise VII, although one might point to the presence of a small echo patch forming he southern edge of the *Calanus* patch. In Cruise VIII, however, there is a marked change patch and *Calanus* patch coincide and aggregation of the echo patches on to the *Calanus* is vivid and complete. The gaps between the *Calanus* patches coincide with gaps in the stribution. The same thing is true of the two patches in Cruise X, but it is less true of the itions in Cruise IX. Here the strongest echo patch is not in aggregation with a *Calanus* it all. This is related in part to a number of traces on the line extending seaward from k-on-Tweed. They were quite dense, but they were all between five and ten fathoms, which usual in this region because the depths of the shoals in general were very variable (Richardson, They could not be identified as fish of a different species, but it is possible that they were fish behaving in a different manner; it is a common observation that one fish species can e to two or three different types of trace, when behaving in different ways (Renou et Tchernia, Marchena, 1951; Cushing *et al.*, 1952).

16 shows an interesting phenomenon. Each picture is contoured using the same contour t is obvious that the densities of the *Calanus* patches increase as time goes on. It is also to rved that the area of each patch becomes smaller as time goes on. The " A " patch in VI–VIII shows this phenomenon quite clearly. The small *Calanus* patch in Cruise VI is k of a distribution that, on the original drawings (see Fig. 8 in Part III), extends right e cruise area, down through three further contour levels. In Cruises VIII and IX (the total









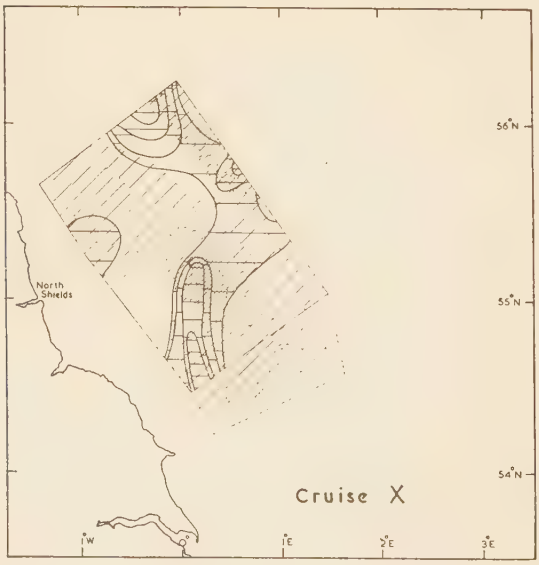


FIG. 16. *Calanus*, STAGE V, AND ECH

The *Calanus* distributions are represented contour levels surrounded by dotted l distributions of echo units are represente contour levels surrounded by full lines.

f which are somewhat less than that of Cruise VI), there were three patches. An analogy
e made with the structure of mountains; the patch of *Calanus* in Cruise VI was like a low
d hill of great extent, but the patches in Cruise VIII were like sharp high mountains packed
ose massif. Thus it appears that the process of aggregation of fish on to *Calanus* patches
e an effect of the relative densities of *Calanus* in space and not of absolute numbers of *Calanus*,
e the low densities in between the peak patches in Cruises IX and X were greater than the
ensities in Cruise VII that must have initiated aggregation. This, of course, assumes that
ere enough fish in the area to make an aggregation.

difficult to understand how this phenomenon of decreasing area and increasing density has
lace. There are three possible types of explanation. First, Professor Hardy has suggested
hat the numbers of *Calanus* are concentrated in area and in numbers by local swirls. This
ttractive idea, which however, cannot be confirmed by hydrographic evidence as taken on
ruises. Or, the effect might be a consequence of aggregation and grazing: that pelagic fish
ggregate on to a patch of food from the edge inwards; the area of the food patch would be
l by grazing at the edge and its density increased in the centre, because the proportion of
s mortality would be least at the centre. Numbers of *Calanus* would be reduced at the edge,
hey were also less abundant originally. The third interpretation is that aggregation on to a
f *Calanus* may be complete, but that recruitment to the larger stages of *Calanus* does not take
t its highest intensity at the same place. One effect of the aggregation of pelagic fish on to
of *Calanus* is that the distribution of fish, and hence of grazing, is always shifting. Patches of
s become split up, much as an infantry company can be broken into pockets, by overwhelming
nstantly changing attack. Recruitment of large stages then possibly does not augment such
s but starts new and ungrazed patches. Because of the continuous movement of the fish,
ould not remain ungrazed for long. It is possible that the decrease in patch size with main-
numbers per unit volume, may be accounted for, by argument of this nature.

OF CORRELATION COEFFICIENTS TO MEASURE AGGREGATION

e XXII gives correlation coefficients between echo units and zooplankton densities. The
rous zooplankton animals investigated were *Calanus finmarchicus* (copepodite stages I–V
ely), *Paracalanus parvus*, *Pseudocalanus elongatus*, *Temora longicornis* and *Evadne nordmanni*;
ere expressed as numbers per m^3. Adult *Calanus finmarchicus* were not included because
nbers of adults caught by the Hensen net were small and were distributed irregularly; this is
s due to heavy grazing by the herring. The echo units (number of echo units per distance
n plankton stations) used in this correlation are those that were assigned to each " echo
"; the zooplankton densities are the means of densities at successive pairs of plankton
. This procedure makes each pair in the two series of values refer to the same position.

l be shown that correlation was generally found between the echo units and the larger stages
ature *Calanus*, at a fairly late stage in the season, but was usually not shown for the other
nvestigated. It is true that there is a significant positive correlation between echo units and
sities of *Temora longicornis* in Cruise VI; there is also a significant inverse correlation between
its and the densities of *Calanus* stage IV. The chart of Cruise VI in Fig. 16 shows that the
y of pelagic fish was concentrated in the south-east corner of the region; this accounts for
rse correlation with the *Calanus* stage IV, the main patch of which existed in the north-west

general conclusion from Table XXII is that apart from the two cases discussed above,
nt correlations are found only with the copepodite stages of *Calanus* in the last three cruises.
r, more important than statistical significance is the magnitude of the correlation coefficient,
is being used to measure the degree of aggregation of pelagic fish on *Calanus*. The mean
the correlation coefficient on stages III, IV, V of *Calanus* during Cruises VIII–X is much
nan that on stages I and II. Again the mean value on stages I and II is larger than that on
nids, during Cruises VIII–X (Cruises VIII–X, the mean correlation coefficient on stages III,
V is 0·3391; that on stages I and II is 0·2545; that on non-calanids is –0·0154). This sums
whole situation quite clearly. We may conclude that pelagic fish were aggregating on to
of the larger copepodite stages of *Calanus*.

ve correlations are found in the calanid sector of the table only during Cruises VIII–X;

Table XXII

Correlation coefficients between echo units and zooplankton densities; Cruises VI–X, 1949, Sir Lancelot

Cruise	*Calanus finmarchicus*						*Paracalanus parvus*		*Pseudocalanus elongatus*			*Temora longicornis*	*Evadne nordmanni*
	STAGES												
	I	*II*	*III*	*IV*	*V*	*IV and V*	♀	*juv.*	♂	♀	*juv.*		
VI (34)	0·1353	0·1962	0·2933	−0·3800*	0·3203	—	−0·1159	0·1168	0·0800	0·1603	0·1758	0·5362†	—
VII (26)	−0·2637	−0·3194	−0·2148	−0·1522	−0·3369	—	−0·0578	−0·1965	0·0398	−0·1726	0·2565	0·2516	—
VIII (32)	0·3184	0·1716	0·4522†	0·1945	0·4424*	0·3219	0·1538	0·2152	0·0401	−0·1249	0·0925	0·0194	—
IX (26)	0·1624	0·3053	0·1637	0·2990	0·2513	0·2041	−0·1978	−0·0518	−0·1221	−0·0647	−0·0127	−0·0962	—
X (17)	0·2513	0·3180	0·4200	0·7024†	0·1268	0·5380*	0·0887	0·0797	0·0439	−0·2524	−0·0520	0·1679	0·1801

*Significant at 0·05 level.

†Significant at 0·01 level.

sely, the fact that 11 out of the 19 correlation coefficients in the non-calanid sector of the or Cruises VIII–X are negative, support the argument that *Calanus* is preferred to non-calanid ods. Fig. 16 shows the relation between the echo units and densities of *Calanus* stage V; XXII extends this relation to the smaller stages of *Calanus* and to non-calanid copepods and that it is limited to the larger stages at this season.

not considered likely that the pelagic fish aggregate on to stages I and II, but that the positive itions between echo units and the densities of stages I and II are a consequence of the fact ney live in the same areas as the older stages. These stages might be eaten, but to a small only, as is shown by Figs. 13 and 14, which show no significant mortality on these stages. 3 and 14 show that the adults, and stages IV and V suffer much heavier mortality than the er stages, therefore it is reasonable to assume that aggregation has taken place on to the s of these larger and oilier animals.

4. Transfer of Aggregation from Stage V to Stage IV

XXII shows that during Cruises VIII–X the correlation coefficients for stage V decline with)·4424, VIII; 0·2513, IX; 0·1268, X); on the other hand those for stage IV increase with time, 5, VIII; 0·2990, IX; 0·7024, X). However, before this transfer in aggregation is considered,

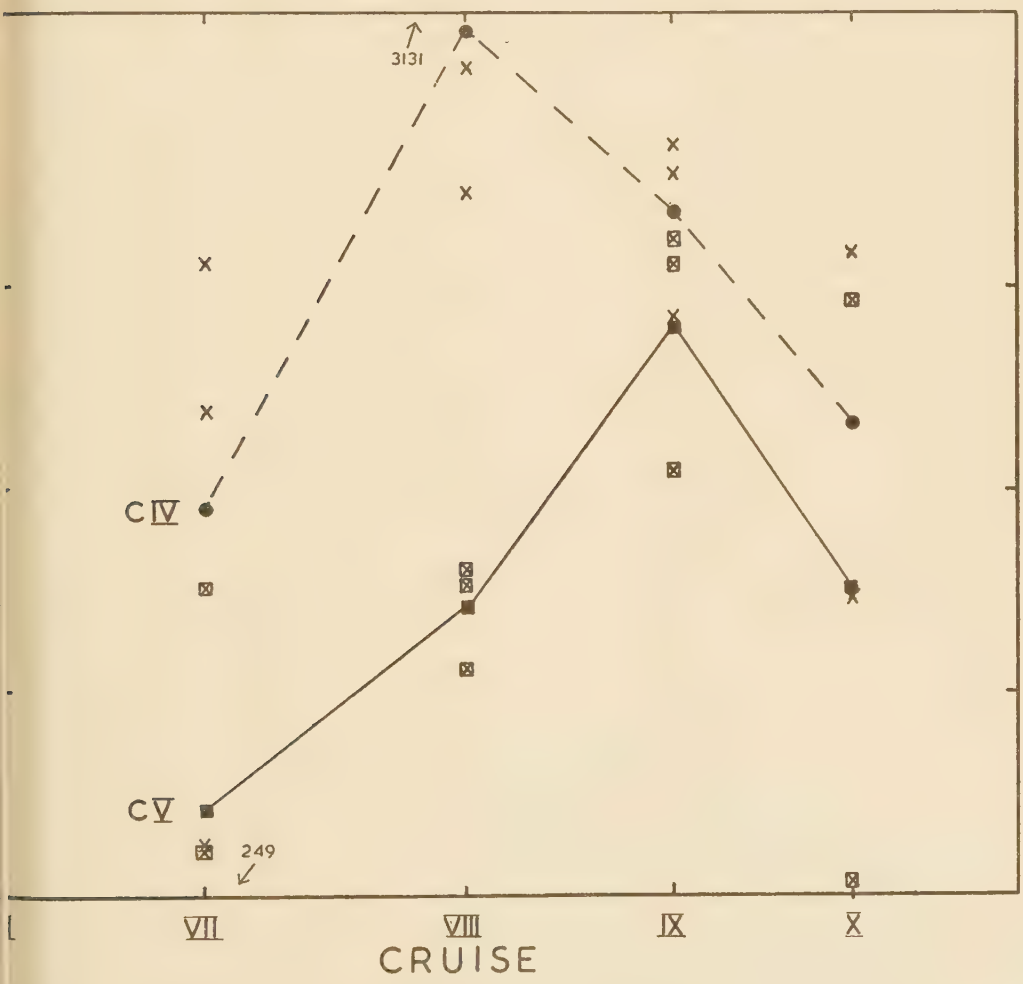


FIG. 17. NUMBERS OF *Calanus*, STAGES IV AND V, IN EACH PATCH ON CRUISES VII-X, SIR LANCELOT, 1949

To obtain actual numbers, multiply by $6{\cdot}4 \times 10^{13}$
Broken line: *Calanus*, stage IV
Full line: *Calanus*, stage V

two limitations must be mentioned of the method of comparing *Calanus* and herring distri
The first is that there must be a certain number of fish in the region that contains the are
Calanus patch, in order that a difference can be established between numbers of fish in the pa
in the region outside it. No estimate is yet available of the numbers of fish that are necessary
an aggregation. The number would be expected to depend partly on the size of the *Calanu*

The second limitation is that we do not know whether the proportion of the total fish po
engaged in an aggregation is high enough to limit the availability for further aggregation.
are a number of fish in the area during the first two cruises, but we have no information a
number of fish outside the area that could come into it. This cannot be estimated until
known about the migrations and composition of the fish populations that come to the are
from Shields in the summer.

Aggregation, as measured by the magnitude of the correlation coefficient between echo u
zooplankton densities, appears to be an effect of the variations in density of larger

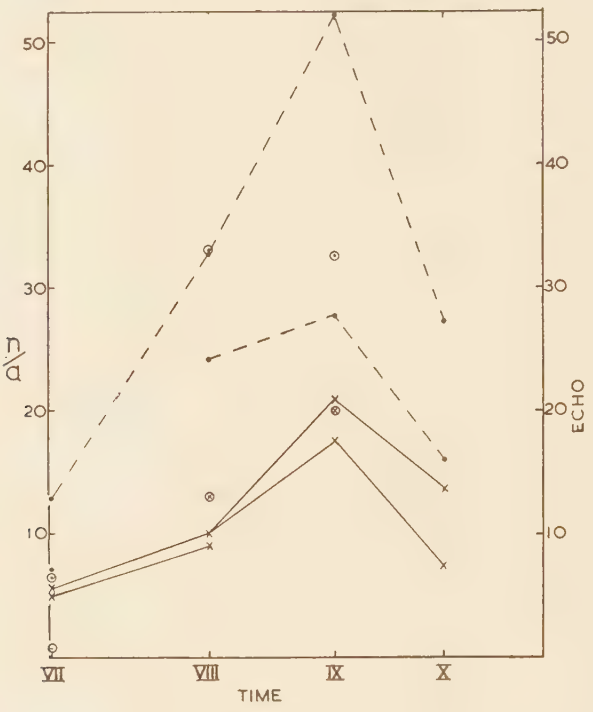


FIG. 18. *Calanus* AND ECHO UNITS IN SUCCEEDING CRUISES

Calanus stage V, for each of Cruises VII–X, is plotted against time as numbers per unit area

x——————x an identified patch of *Calanus* V
⊗ an unidentified patch of *Calanus* V
•----------• an identified patch of echo units
⊙ an unidentified patch of echo units.

copepodite stages over the area of survey. However, it might alternatively be an effect
numbers, i.e., a large area of low numbers might be as effective as a small area of high
From the pictorial representation in Fig. 16, it does seem, however, from the phenom
decreasing size and increasing density that a small area of high numbers is more effectiv
large area of low numbers, i.e., that high density is an effective factor.

Aggregation is not, however, a simple effect of high density of *Calanus*. Fig. 17 sh
numbers of *Calanus* IV and *Calanus* V in each patch for each of the Cruises VII–X; the rer
point is that there are twice as many stage IV's in Cruise VIII as there are stage V's. *Calanu*
is about $1\frac{1}{2}$ times the size of *Calanus* stage IV, so the biomass of stage IV in the area wa
than the biomass of stage V. The initial aggregation, however, as measured by the co
coefficient in Cruise VIII takes place on the stage V. Subsequently in Cruises IX an
difference between the numbers of *Calanus* stage IV and *Calanus* stage V becomes ve
reduced, yet aggregation becomes transferred to the smaller stage IV. Again Fig. 17 shows

ers of *Calanus* fall from Cruise VIII onward, yet it is from this time that *Calanus* IV becomes eferred stage. Thus the direction of the transfer of aggregation runs counter to the direction nge of biomass.

regation, or the gathering of fish on to food patches, is shown not to be an effect of numbers biomass of the food. Let us suppose that the fish were moving randomly in direction and stant speed, and that they slowed down to feed; then fish would aggregate on to the food es. The extent of aggregation would depend upon the time the fish spent feeding—i.e., the rtion of time spent stopped in a given period. One might imagine that fish would be slowed re effectively by a sudden change of food density on their course, than by a slow change. ossible that the transfer of aggregation from *Calanus* stage V to *Calanus* stage IV can be ed to the relative steepness of the slopes of the contoured charts for the two stages; the transfer regation may then depend upon the different rates of increase of numbers of food organisms it distance.

re is some information on the decay of aggregation. Fig. 18 shows the numbers per unit f *Calanus* stage V in patches, plotted against time; the figure also shows the numbers of echo per unit area plotted against time. Cruise VI has been excluded because there was no clear

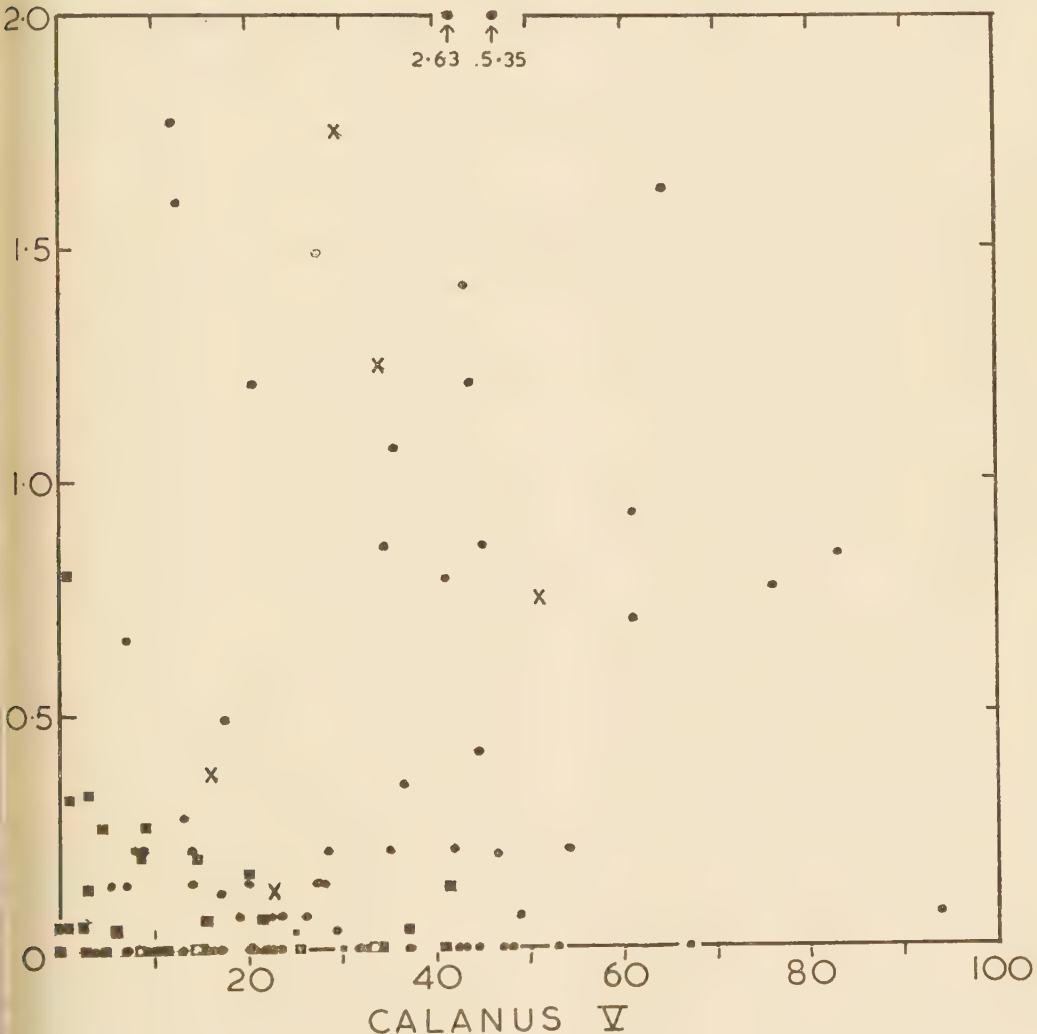


FIG. 19. ECHO UNITS AND DENSITY OF *Calanus*, STAGE V

Density of *Calanus* stage V is expressed as numbers /m³.
● Observations from Cruises VIII–X, SIR LANCELOT, 1949.
■ Observations from Cruise VII, SIR LANCELOT, 1949.
× Average numbers of *Calanus* /m.³ per level of echo units.

trace of aggregation taking place. Numbers per unit area have been used here, because t marked differences in areas of the patches in all of the later cruises. This shows that the of echo units present in the patch areas reach a peak in Cruise IX and subsequently decli suggests that aggregation dies away when numbers of *Calanus* start to fall.

Disengagement, or the dispersal of fish from food patches, possibly does depend upon the of the food per unit volume; this is, in effect, the numbers remaining after intense predatio fish. Hence, there is likely to be a proportion of numbers of fish to numbers of *Calanus* volume, at which disengagement takes place.

It may be useful to consider the whole process as taking place in two phases, aggrega disengagement. In the meanwhile, it is possible to take the examination of the presen little further.

5. The Form of the *Calanus*-echo Relation; Aggregation and Disengagement

The observations will now be examined in a little more detail on the interpretation that agg depends on a gradient in density of food from place to place. The possible effect of the tw of aggregation on the recruitment and mortality of *Calanus* will be shown, and the part agg plays in the dynamic cycle will be demonstrated.

Figs. 19 and 20 show all observations used in the relation between echo units and num of *Calanus* stages IV and V. From these observations, it is possible to find the depen

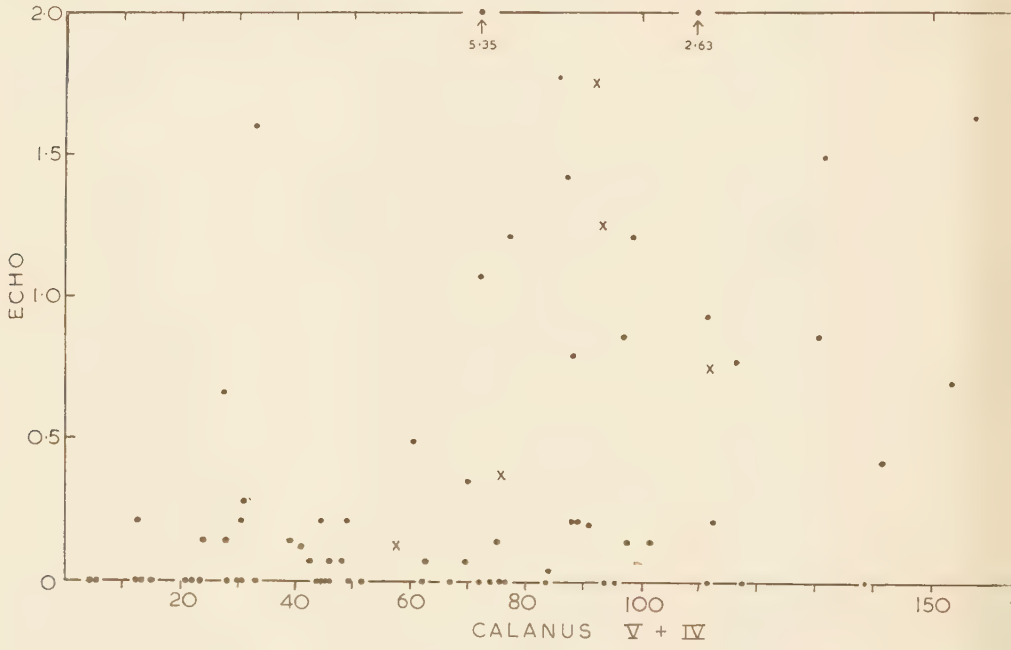


FIG. 20. ECHO UNITS AND DENSITY OF *Calanus*, STAGES IV AND V
Observations from Cruises VIII–X, SIR LANCELOT, 1949, are used.
x Average numbers of *Calanus* /m.³ per level of echo units.

numbers of echo units on numbers of *Calanus*/m³. Such dependences are shown in Figs e.g., in Fig. 21 the mean number of echo units for levels of *Calanus* stage IV, 0–10, 10–20, 20 are plotted. In Figs. 21 and 22 it will be noticed that the highest mean echo value is fo middle density of *Calanus* (the single observation at 150 *Calanus*/m.³ in Fig. 21 is disregar

As aggregation proceeds, food patches must become split up, and the regions of high are grazed down to regions of middle density. So a high *Calanus* observation is one escaped predation. As the aggregative process grows older, such observations would bec common. It appears that aggregation started on *Calanus* stage V, when these reached a of 30–40/m.³; aggregation transferred to stage IV from stage V when a greater range of per unit distance appeared in stage IV (Cruise IX, the range in n/m.³ of *Calanus* V was t that for *Calanus* IV was 1–150); disengagement took place when the density of *Calanus*

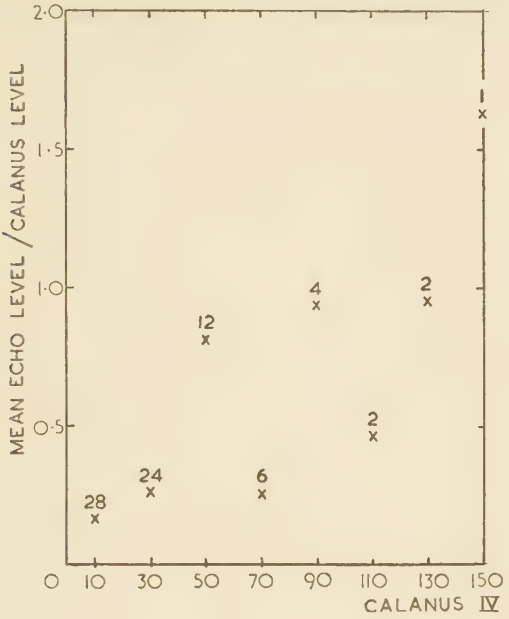


FIG. 21.

ıo units are expressed as the mean number per level of numbers /m.³ of *Calanus*, stage IV. The levels of *Calanus* numbers used are 0–10, 10–20, 20–30/m.³, etc.

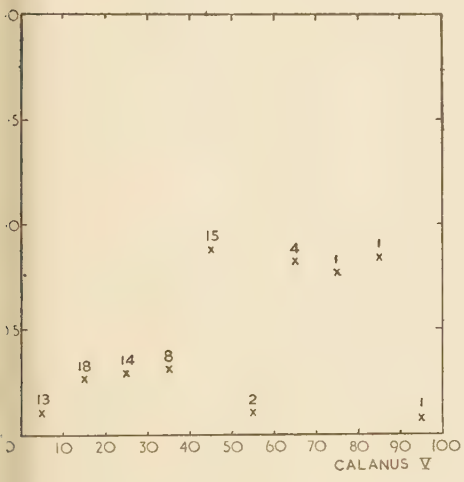


FIG. 22.

Echo units are expressed as the mean number per level of numbers /m.³ of *Calanus*, stage V. The levels of *Calanus* numbers used are 0–10, 10–20, 20–30/m.³, etc.

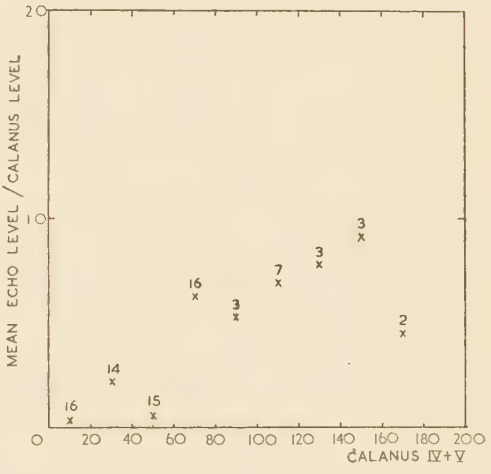


FIG. 23.

Echo units are expressed as the mean number per level of numbers /m.³ of *Calanus*, stages IV and V. The levels of *Calanus* numbers used are 0–20, 20–40, 40–60 /m³.

g. 18). To sum up, it seems possible that there may be an initial density in numbers at which ıtion takes place, that subsequent changes in aggregation are related to the relative rates of of numbers per unit distance of the different foods and, lastly, that disengagement takes hen fish no longer get a full ration.

age distributions of *Calanus* stages in Figs. 13 and 14 (see p. 32) may now be re-examined. noticed that the mortality of *Calanus* stages IV and V was much greater than that of the tages. This is not necessarily related to grazing by the herring, but in view of the correlation ents expressing aggregation, it seems that it may be very likely.

The second point is that the recruitment to the larger stages manifestly decreases very This may be attributed to any one of three factors: (1) the decrease in egg production d decrease in numbers of plants available for food (see Marshall and Orr, 1952); (2) the de egg production due to a severe reduction in the number of adults—which is unlikely as the of adults is constantly low; (3) a severe mortality on the naupliar stages, associated with the in numbers of predators. There is no means at the moment of distinguishing between thes but it is clear that the sharp decrease in recruitment did take place.

The third point is that the numbers of adult *Calanus* in Cruise X increases sharply; it is five-fold increase, compared with the previous cruise. If one admits that the lack of nu adult *Calanus* in Cruise VI was merely the small numbers at the start of the season, the be that this increase in the number of adults is associated with the decrease in the nu herring.

These three points emphasize the three factors that are important in this work—the repr rate of the *Calanus*, the mortality rate of the *Calanus*, and the aggregation—disengagemen of herring numbers, the last of which controls the number of *Calanus*.

6. Analogy between the Drifter-herring Relation and the *Calanus*-echo Relation

The aggregation of drifters on to patches of herring is substantially the same problem as t gation of herring on to patches of *Calanus*. Drifter landings are reported daily as catch at a particular position. These positions are later recorded (in crans) in 10-mile statistical It is possible to use the mean catches per square per night as an index of herring ab analogous to the catch of *Calanus* per m.^{3} at each station. Then the number of drifters p per night may be used as an index of abundance of drifters comparable to the number of e per " echo station ". Again, the searching by pelagic fish for their food corresponds to t searching for fish, resulting from the spread of information in the fleet. Herring eat *Cal* drifters catch herring; herring aggregate on *Calanus* patches and drifters aggregate on fish Subsequently, pelagic fish disengage from grazed *Calanus* patches and the drifter fleet d from an exploited fish patch. Both the *Calanus*-herring relation and the herring-drifter rel the result of the balancing of three processes: (*a*) rate of change of numbers of the pred process of aggregation; (*b*) the rate of change of numbers of the prey due to reprod immigration; and (*c*) rate of change of numbers of prey due to predation and the conseque of numbers of the predators.

There is an important difference in method between the *Calanus*-herring analysis and the drifter analysis. The *Calanus*-herring relation has been described by plotting numbers o against numbers of echo units. The drifter-herring relation is described by comp catch/square with the number of boats/square. These observations are not independent echo and *Calanus* observations. This has been partially overcome by using echo survey independent estimates of the abundance of herring.

Fig. 24 shows the relation between the number of boats and the mean catch per 10-mile s three conditions; (*a*) the November shoals in East Anglia; (*b*) the October shoals in Eas and (*c*) the feeding shoals off Shields. The figure shows the relation between the abundan and the abundance of drifters. Each graph in the figure shows two regressions: (*a*) a linear r of the number of boats per square on the mean catch per square; and (*b*) a curvilinear regr the mean catch per square on the number of boats per square. The first regression s condition of aggregation and the second shows an estimated distribution of the abundanc It will be seen that the dependence of the number of boats on mean catch may be direct (N in East Anglia), may be inverse (North Shields), or the two variables may be independent East Anglia).

Fig. 24 shows three conditions: (*a*) that, in the East Anglian fishery in November, the positive regression of the number of boats/square upon the mean catch/square; (*b*) tha North Shields fishery in May, there was a negative regression of the number of boats/squ the mean catch/square; and (*c*) that, in the East Anglian fishery in October, there is an inte case, there being no regression (it is positive, but not significant).

When the catch decreases with increased number of boats, as at Shields, there are thre explanations; (*a*) fish may be leaving the area of fishing; (*b*) drifters close to each oth drive fish either into the nets or away from them; and (*c*) the fish shoals are being re

g. The first two possibilities are the same because any emigration must be from the areas drifters congregate; as these areas are not the same from one day to the next, the cause of ation must be the drifters themselves. Any effect due to the drifters being close together l be expected to increase catches and not to decrease them. Hence, the third possibility is the one—that the shoals are being reduced by fishing.

en the catch increases with the increased number of boats, there are two possibilities: (*a*) that y set drift nets drive fish into the nets; and (*b*) that the fish shoals are very large and the fleet ays searching and finding the regions of abundance. These are always changing, so the mean does not decline after a short period of fishing, because in that period new searches have been

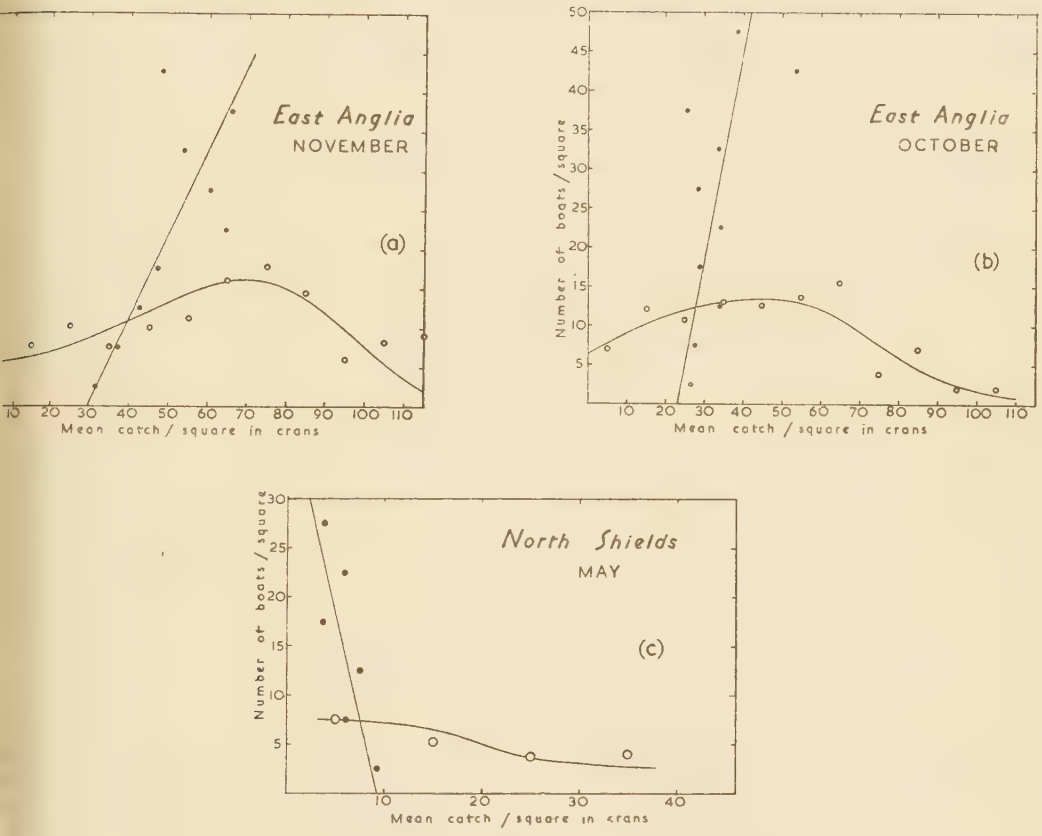


FIG. 24. AGGREGATION OF DRIFTERS ON THE HERRING

.e linear relation shows the dependence of the number of boats per statistical square upon the mean ıch/square. The curvilinear relation shows the dependence of the mean catch per square upon the number of boats per square.

In other words, the process of searching overshadows the effect of fishing. Of these alterna- the first is unlikely because drift nets are closer together in October than in November (cf. the ıum number of boats/square in October and in November, Fig. 24).

May, off Shields, shoals are small (mean catch is 6 crans); little searching takes place and the ctive effect of fishing shows quickly. In November, off East Anglia, shoals are large (mean is 52 crans) and searching is predominant to the effect of fishing.

as been mentioned that as catches of herring and numbers of boats are obviously related, ependent estimate of the abundance is necessary. During October, 1951, an echo survey was in the area Whitby—4° E, Texel, Ijmuiden, Lowestoft. This was carried out as a grid with tudinal lines 20 miles apart. From these results it was possible to make an estimate of the ɛr of echo units/10-mile square. Each 10-mile square on the chart was measured with a ıeter, and the parts of each square at different echo levels were raised by the appropriate ensity. For the period of the cruise (9th–17th October, 1951) the 10-mile squares were assigned

to three different levels of abundance, estimated by echo survey. The results are shown in these are virtually the same as the results given in Fig. 24. This confirms the former resu the use of independent observations.

Fig. 26 shows the relation between the number of boats/square and the coefficient of v of the catches/square; as in Fig. 24, the three parts refer to the East Anglian fishery in No and October 1951 and the Shields fishery in May 1949. The coefficient of variation was u measure of the " lumpiness " of which fishermen often talk. At Shields, there are positive reg of the number of boats on the coefficient of variation. Thus the coefficient of variation of increases with the increasing numbers of boats. At East Anglia, the conditions are quite d there is no regression of numbers of boats on coefficient of variation in either October or No It is concluded that at East Anglia there is no relation between the number of boats and efficient of variation of the catches. It will be remembered that the main difference betw East Anglian condition and that off Shields is that off Shields the mean catch is reduced

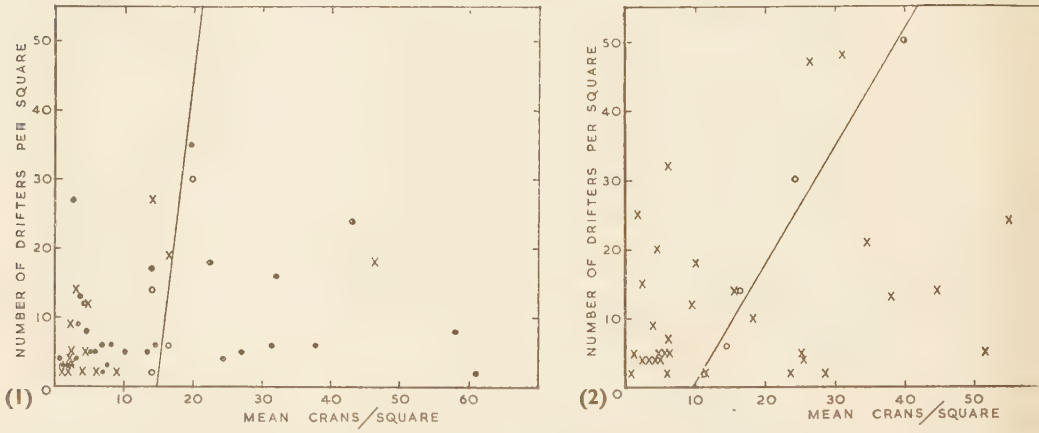


FIG. 25. AGGREGATION OF DRIFTERS ON THE HERRING AT DIFFERENT LEVELS OF ECHO DENSITY

(1) 0–2,500 echo units per statistical square: × = 0–1,000 units; • = 1,000–2,500 units.
(2) 2,500–3,500 echo units per statistical square.
Regression lines show the dependence of the number of boats on echo density; points shown b

increased number of boats, whereas the reverse is the case off East Anglia. Thus, it is pos this exploitation of small shoals is associated with an increased " lumpiness ", due to th being split or dispersed.

The analogy between the drifter-herring relation and the herring-*Calanus* relation may in the following way. It was noticed that the highest echo values were only found at *Calanus* level. Considering the very much smaller number of observations available for t *Calanus* comparison, Fig. 22 is not unlike the dependence of mean catch/square upon the n boats/square. It is probable that the range of aggregative states is much greater in Fig. 2 because it extends over six weeks and partly because the differences between the rates of the p (*Calanus* reproduction, herring aggregation, *Calanus* mortality and herring grazing and disengagement) are very much greater. Thus it is not to be expected that the echo-*Calanu* should be as clear cut as the drifter-herring ones. The point of the analogy lies reall dependence of the number of boats/square on the mean catch. This is comparable to the re of mean echo level upon *Calanus* density.

Associated with the decline of mean catch with increasing number of boats at Shields increased coefficient of variation with increasing number of boats. As fishing reduces th they become more " lumpy " or more variable in size. Applying this theme to the *Calanus* one might expect that the patches become split up, producing more steep gradients in r increasing aggregation and predation. Thus we might expect that a transfer of aggregatio effect of predation.

Hardy *et al.* (1936) have suggested that by the use of the *Calanus*-herring relationsh possible to increase a drifter's catches. They have shown that there are sometimes si

tions between *Calanus* and herring, but that quite often the associations are negative. The s expected if the herring eat *Calanus* at all destructively. Thus the method has to be used y, because a high *Calanus* concentration may only mean that fish have not yet reached it erefore it is not worth fishing there. Conversely, a nil *Calanus* indication may mean a good because the fish are there in numbers sufficient to have eaten all the *Calanus*. This is only e problem, because any catch of herring depends partly upon the abundance of the herring rtly on the drifter-herring search situation. Over a period the catches of any drifter would nged in one of the three states shown in Fig. 24. Thus a high or low catch could be merely

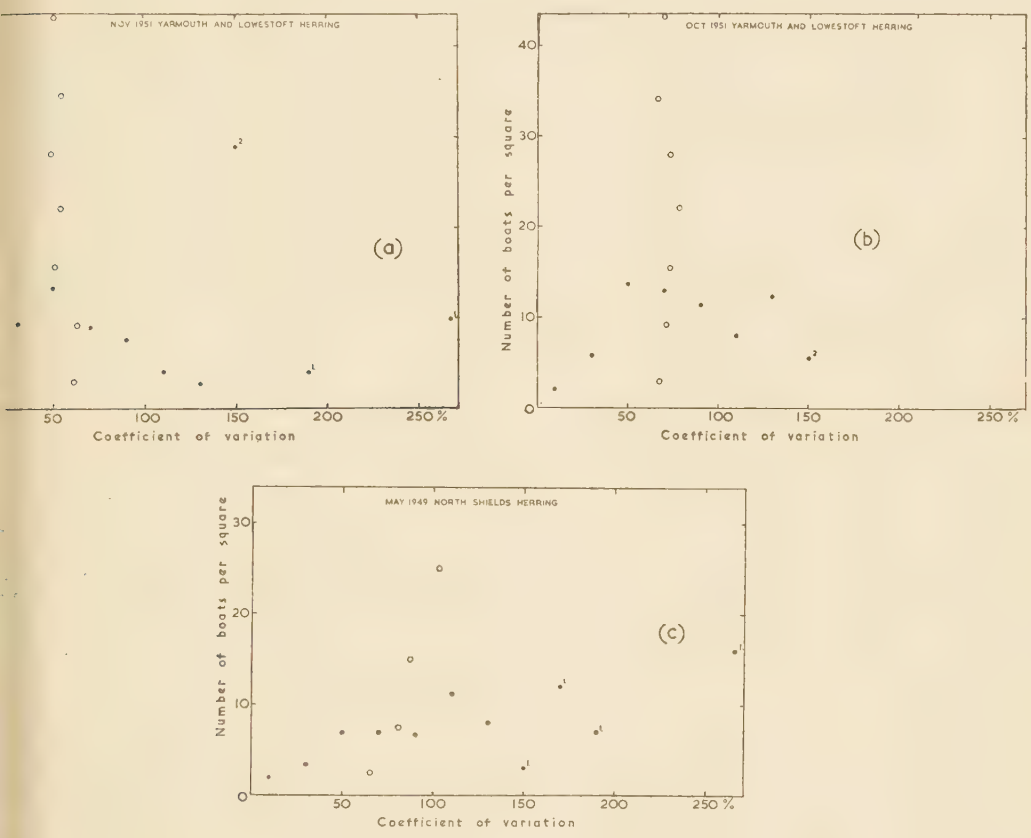


FIG. 26. AGGREGATION OF DRIFTERS AND PATCHINESS OF CATCHES

on of the aggregative state of the fishery. If the herring have aggregated on to *Calanus*, a association between *Calanus* and herring catches may be the result of efficient searching, egative association may be the result of exploitation by the fleet of a patch of herring in the tive state on the *Calanus*.

7. Movements of the Fish Shoals

positions of the fish may be deduced from the echo pictures in Fig. 16 (p. 38). In Cruise VI own that there is a concentration of fish along the north bank of the Dogger; the same ment, a little diluted, occurs in Cruise VII. The same observation was made in March and 948. These fish were not scattered in the midwater in small shoals but were on the bottom dense shoals. The distribution of the echo patches in Cruises VII and VIII suggests that some great population of fish in what might be termed the North Dogger reservoir. gh there is no independent evidence for such a reservoir, there is circumstantial evidence in ho pictures for Cruises VI, VII and VIII. *Calanus* patches are then carried south as would cted from consideration of the normal drift. A complicating factor is that in the later (VIII, IX and X), *Calanus* patches are drifted in from the north-east, which have echo

patches in aggregation. Such events could explain the mixed character of the Shields f fish can appear from the south and from the north-east.

We may believe, however, that the duration of the period of aggregation of herring *Calanus* patches may depend on the dynamics of the aggregative process. Then, the distanc which the fish travel in aggregation would depend on the numbers of *Calanus*. This wo two effects:

1. The fish from the North Dogger reservoir, which we shall call the " indigeno would be carried away from the area through distances dependent on the rates involv aggregative processes.

2. Fish from the north-east, which we shall call " invaders ", would come into the a distances dependent upon the numbers of *Calanus* further " upstream " at the time of agg

This may be summarized in this way. In a year when *Calanus* production is small, th fishery will mainly consist of North Dogger reservoir fish going from small aggregation aggregation within this area; on the other hand, when the *Calanus* production is high, th fishery will consist of populations that come from a great distance and with those from t Dogger reservoir will be carried away towards the German and Danish coasts. This coul a mechanism by which stocks become mixed in the central North Sea in the summer.

As the season advances there is a little evidence that the size of shoal increases, judgi average size, in number of soundings on fish, of the actual shoals recorded on the ech paper. Table XXIII gives this for Cruises VII–X.

Table XXIII

Mean shoal size in number of soundings

Cruise			
VII	*VIII*	*IX*	*X*
2·11	2·27	4·60	4·27

If this increase in size of shoal is a real one, and in the later cruises there is also an incre number of large shoals, which do not exist in the early cruises, then it seems that a co of the grazing and searching within the aggregations that have been described, is the thi the shoals.

8. Summary

Part IV may be summarized in this way:

1. Pelagic fish move into the area from the northern edge of the Dogger in April.

2. They aggregate on the southbound patches of *Calanus* in May, first on stage V at of about 30/m.^{3} over an area of about 100 km^2.

3. As aggregation on to stage V tends to decrease, it is replaced by aggregation on t and possibly even to stage III, and in a poor year on to *Temora* and smaller copepods. of this shift in aggregation will depend on the original numbers of stage V's and their ca satisfying the hunger of the numbers of herring aggregating.

4. As a consequence of grazing, numbers of stages IV and V decline and aggregation ceases. Shoal size increases.

5. The existence of a reservoir of herring north of the Dogger Bank, the southbound s the extent of aggregation, could provide a mechanism for mixing shoals and perhaps s extent of the mixing being dependent mainly upon the numbers of *Calanus* in patche Fraserburgh and Shields.

Part V

The Relation of the Diatoms to the Herbivores and to the Nutrients

1. Introduction

ossible foods of *Calanus* during the spring and early summer are diatoms, dinoflagellates and ellates. Of these, it is believed that diatoms are the most important food organisms. Marshall) has shown that diatoms are commonly found in the guts of *Calanus* at this season; twenty- diatom species have been found in the guts of *Temora longicornis* (G. C. Trout, personal unication). During the period covered by these cruises, dinoflagellates were uncommon in ater-bottle samples (although predominant in Cruise IX in the Fine Net). Although *Calanus* ibsist on a diet of μ-flagellates, these small plants are probably not their main food, for the ns given in Part II. Table III (in Part II) shows that in terms of plant volume/litre, the diatoms ddle size are the most important; in numbers, however, this is not so. Filter-feeding animals ake a proportion of the smaller diatoms, but the middle-sized diatoms might only be taken pture, because they are more thinly distributed; the same might be said to be true of small ed diatoms. The assumption here is that feeding takes place partly by acts of selective food re and not completely by filter feeding; this is borne out by Harvey's (1937) experiment ng that *Calanus* " preferred " the larger *Ditylum Brightwellii* and *Lauderia borealis* to the r *Nitszchia closterium*. When its food is abundant, one might imagine that *Calanus* feeds on ants that it finds within the range of one hop; as it is a large copepod, its hops would be long ight approximate to the mean distance between the middle-sized diatoms during Cruise VI. rly, one might expect that small diatoms would become the food of smaller copepods. *ria borealis* at a density of 2,244/litre in Cruise VI is likely to occur once every centimetre of movement; *Thalassiosira gravida* (23,581/litre) and *Chaetoceras compressus* (9,281/litre) occur at a density of two or three for every centimetre of linear movement, if they lived ndently, but when in chains, at a density of 1 chain for every 3 or 4 centimetres of linear nent. *Ditylum Brightwellii*, however, a very much larger diatom (219/litre) will occur once 2 centimetres of linear movement. One might expect that *Calanus* when feeding on these e-sized diatoms would make hops of between one and five cms.; a smaller copepod, e.g., *calanus*, might make hops about $\frac{1}{2}$ cm. to 2 cm. This is only an average statement and takes count of the patchiness of marine organisms. Thus, it seems probable not only that *Calanus* ts mainly on diatoms but that it may prefer the middle-sized ones, which make up the bulk plant volume/litre.

Calanus/diatom relation cannot yet be solved by analysis of gut contents because nothing wn of *Calanus* digestion rates; in the meanwhile, gut contents are useful in showing the rtions of various foods consumed. There are, however, two problems that are of greater t. The first is the total quantity of food that the *Calanus* populations consume and the l is the rate of change of the counted numbers of diatoms in the sea. The latter is important, e when the numbers of diatoms in the sea decline, a limit may be set to the quantity of food ble to the *Calanus* populations. In view of the relation between available food and egg ction shown by Marshall and Orr (1952), this may consequently set a limit to the recruitment *Calanus* populations.

first problem, the quantity of food consumed by *Calanus*, is solved by attacking the second, e of change of the counted numbers of diatoms in the sea. If the division rates of the diatoms own and the grazing rates of the herbivores are known, the produced numbers of diatoms estimated after any time interval; the difference between produced numbers and counted rs after this time interval is the quantity that has been consumed by herbivores, added to antity that has died " naturally ". " Natural " mortality is mortality that is not attributable zing by the herbivores. The diatom population may be described dynamically in terms of vision rates of the diatoms, the grazing rates of the animals and of the natural mortality rates

of the diatoms. It is this sort of equation that Fleming (1939) devised to deal with the produced by Harvey *et al.* (1935). There are three factors in the equation and their determ presents difficulties. The first is how to assign a suitable rate of grazing. The choice affe formal integration, but need not be dealt with here. For the moment the quantity graz be estimated as a function of the difference between the quantity produced and the quantit " naturally ". The second difficulty lies in the estimate of natural mortality which Fleming ig this will be derived from dead cell counts. The third difficulty is in estimation of the divisi Up to the present, this has been done indirectly. Riley *et al.* (1949) have substituted for the c rate a production increase coefficient, which is a complex of factors that includes the photosy rate, the respiration rate, the effects of temperature and radiation changes, the effect of n depletion and of turbulence. These all affect division rates, but none are directly measurabl sea without many observations and many experiments. The rate of photosynthesis may be est from the use of black and white bottles hung in pairs at short intervals of depth down to th pensation depth; such an experiment takes twenty-four hours, and obviously at least one obse per cruise would be needed for any area that is being surveyed.

In this section an estimate of division rate will be used, which is the result of changes in ra photosynthesis, temperature, nutrient supply and turbulence. Using this estimate, an ass of production will be made, which is the first step in any analysis of the dynamic cycle.

2. Estimation of the Division Rates of Diatoms

(*a*) EXPERIMENTS UPON THE DECREASE OF CELL WIDTH PER DIVISION

Wimpenny (1936, 1946) and Lucas and Stubbings (1948) have made many measurem marine diatom populations, yielding distributions, most of which are markedly polymod decrease of cell width of *Rhizosolenia styliformis* with time over a long period is clearly Although the intention was to use the sizes of diatoms as markers for plankton patch

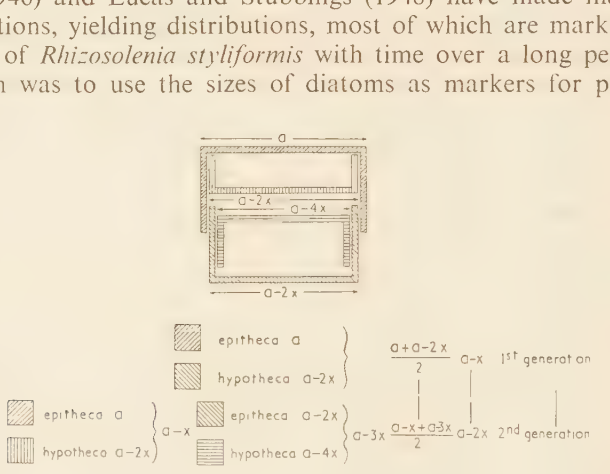


FIG. 27. THE DECREASE OF DIATOM CELL WIDTH AT DIVISION

As any measurement with a light microscope in transapical width is the mean of the epithecal and hypoth width, the difference in mean width between each division is one cell wall width, x. The measureme the first generation cell is $\frac{a + a - 2x}{2}$ or $a - x$; the measurement of the second generation ce $\frac{a - x + a - 3x}{2}$ or $a - 2x$, where a is the width of the parent cell.

suggest the possibility that the cell width decrease of diatoms might give an index of the of divisions that the population has undergone within a given period of time.

When a diatom divides into two daughter cells, one is of the same size as the parent, as m across the transapical axis, and the other is slightly smaller. Thus, as division proceeds, tl of diatoms should become smaller and smaller in size. Between one generation and the difference in size across the transapical axis is the thickness of one valve wall. This point easily illustrated in a figure—(Fig. 27). Hence, between two cruises, the difference in s diatom species divided by the thickness of the valve wall, will give an estimate of the nu divisions that have taken place between the cruises. This neglects any elasticity in the sil of the marine diatom, any variations in its thickness and any variation in wall thickness

luals. It must also be assumed that the population of the diatom species may be identified cruise to cruise. This is permissible if we can assume that diatom patches move in much the general way as copepod patches, and that patches identified between cruises by copepod vill include the same diatom populations.

senburg-Lund (1908) measured the decrease in the transapical axis of various diatoms, over od of time. Among others, size distributions of *Melosira* and *Asterionella* were made; these ometimes unimodal, sometimes polymodal and sometimes skewed, but it is clear that there marked decrease in median size as divisions proceeded over a period of time. His observations derstandable, when it is remembered that the original size, as transapical width, is restored process of auxosporing. *Sceletonema costatum* has been observed in the act of auxosporing. lica wall breaks, the cell itself bubbles out into the gap, often in a spherical form, which gradually ns out into a new shape, the transapical axis of which is now maximal. The size decrease again at the first subsequent division. There is a little evidence that cells auxospore when a al size is reached, but there is none about the largest size that may be reached during the s of auxosporing; indeed I have observed a cell of *Biddulphia sinensis* to auxospore twice in succession. Thus, a size distribution of diatoms is being replenished with large auxospored t the upper end of the scale, continuously or perhaps periodically; and, by the same process, pulation loses individuals from the small end of its scale in size. So, in practice, distributions ten polymodal.

ne tests of the ideas given above have been carried out by means of culture experiments. it is necessary to show that division is really accompanied by a decrease in transapical width, se it is known that some pennate diatoms can reproduce for perhaps years with little measurable e in cell size (Wiedling, 1948, on *Nitszchia palea;* Wilson, D. P., 1946, on *Nitszchia closterium minutissimma*). An opportunity to do this arose in the summer of 1948 with a culture of *onema costatum.*

original diatoms were taken in a Fine Net sample off Flamborough Head and were brought o the laboratory in Miquel sea water; they were transferred ashore into Erdschreiber. It en found that there was a greater initial mortality of diatoms (particularly *Biddulphia sinensis*) ischreiber than in Miquel sea water. After a time, a monospecific culture of *Sceletonema um* developed; these were grown in wide-mouthed culture flasks suspended before a slightly west window. In front of this window hung a short black curtain that excluded direct light lowed the breeze to agitate the flasks. The temperature under these conditions varied between and 21° C. over three months.

s were measured with the Reichert binoculo-monocular microscope ($\frac{1}{6}$ objective and $\times$ 10 ces) and a blue filter was used in the condenser. Each size observation was the mean of asurements; these were made in the centre of the field to the nearest half division on the ce scale. The cultures were counted with a haemacytometer; they were originally counted ins, but as the number of cells per chain varied with the division rate, this was abandoned bsequently cells were counted instead.

le XXIV shows the cell sizes (the transapical widths) of cultures C, U and S in eyepiece units the months of August and September, 1948. The table also shows the numbers in each expressed in logarithms, during the same period. In both parts of the table, the rapid periods are enclosed between lines, drawn from the change in log numbers and transferred columns of cell width.

measurements during the period of rapid growth have been used to find the cell width decrease g population increase, which bears a constant relation to the cell width decrease per n. Only the periods of rapid growth are used, because when growth slows down, cells sink e size distribution changes, giving a different mean size. This effect of cells sinking after a of rapid growth is described by Karsten (1898). Karsten also showed that after rapid n, the cells lost their silica rods; Braarud (1948) found that this was due to silica deficiency. ltures were grown in soft glass flasks and the silica rods were always visible, so there was no leficiency. However, the chloroplasts in the cultures were very large. Under the conditions experiments, growth was often a function of temperature and as this varied from day to day, the growth-rate. Thus periods of rapid growth tended to be rather short.

le XXV gives the cell width decrease for the three cultures. For the periods of rapid growth, ere fitted to the decrease of cell width with time, by least squares; by the same method, a is fitted to the increase in log numbers of the population.

Table XXIV

Reduction in cell width with increase in numbers for the three cultures, C, U and S

1948	*Cell sizes in eyepiece units; each observation is the mean of 50 measurements*			*Log numbers of each culture*		
	C	*U*	*S*	*C*	*U*	*S*
June 7	2·31			2·61		2·57
,, 8	2·37			2·84		2·53
,, 9				2·92		2·58
,, 10				2·86	1·68	2·57
,, 11						
,, 12	2·08	3·71	2·08	2·85	1·51	2·67
,, 13						
,, 14	2·05	3·44	2·62	3·23	1·72	2·60
,, 15	2·06	3·34	2·20	3·17	2·11	2·74
,, 16	2·01	3·43	2·04	3·39	2·38	2·83
,, 17	1·94	3·28	2·08	3·33	2·57	3·03
,, 18	1·91	3·01	2·00		2·67	3·11
,, 19	1·90	3·01	1·95		2·71	3·21
,, 20						
,, 21			1·79		2·76	3·28
,, 22					2·91	3·31
,, 23			1·87		2·80	3·39
,, 24			1·76		2·67	3·43
,, 25		2·86	1·74			3·49
,, 26		2·92	1·75			3·52
,, 27						
,, 28		2·84	1·73			3·53
,, 29		2·81				
,, 30						

1 eyepiece unit = 3·17μ

Table XXV

Derivation of cell width decrease/division for *Sceletonema costatum*

	C	*U*	*S*	
a_1	−0·039	−0·094	−0·041	Regressions of cell size (Y) on days (X)
a_0	2·381	3·581	2·174	
a_1	0·068	0·195	0·070	Regressions of log numbers (Y) on days (X)
a_0	2·617	1·678	2·762	

	—in eyepiece units—			1 eyepiece unit = 3·17μ		
	C	*U*	*S*			
Cell width decrease per day	0·0393	0·0940	0·0411			
Log numbers increase per day	0·0675	0·1949	0·0700			
Cell width decrease / Log numbers increase ..	0·582	0·482	0·587	*— in μ —*		
				C	*U*	*S*
Cell width decrease per division	0·175	0·145	0·177	0·555	0·460	0·561
Mean cell size	2·12	3·25	1·94	6·72	10·30	6·15

ıese methods, the decrease in cell width and the increase in log numbers for the same period ne were obtained. The third line of the lower part of the table shows the cell width decrease ›g population increase; which is converted to cell width decrease per division in the fourth line. :onversion constant can be found to be log 2, deriving from the fact that numbers are doubled :h division. As the cell width decrease for each division is equivalent to the cell wall thickness ıean value for the cell wall thickness derived from these results is 0·53μ. If, instead of the ase in numbers, cell thickness was independently known, the calculation would yield the ›er of divisions that had taken place. This is how cell size decrease can be used to estimate on rate and, so, production.

second series of experiments was carried out on a culture of *Biddulphia sinensis* in 1950. The re was maintained in Erdschreiber in an artificially lit refrigerator at a constant temperature ° C. The cells were measured with a phase contrast microscope ($\frac{1}{3}$ objective × 10 eyepieces) ı screw micrometer. Samples were counted in a watch glass in a measured quantity of culture um. Three cultures were maintained during a rapid growth period of 5 days. Table XXVI gives ean cell widths of the three cultures during the period. The table also shows the daily counts of ells. From this information, the cell width decrease per division is derived; from the three res, a mean value for the cell width decrease per division is given in μ. From these experiments ›ears that the cell wall width of this diatom is as large as 1·30μ.

Table XXVI

Derivation of cell width decrease/division for *Biddulphia sinensis*

	Cell widths in eyepiece units			Log numbers of each culture		
	Cultures			*Cultures*		
	1	*2*	*3*	*1*	*2*	*3*
1950						
July 29 ..	100·12	101·94	105·32	1·7243	0·6812	1·0212
,, 30 ..	100·12	93·44	105·46	2·0588	0·8633	1·2900
,, 31 ..	97·56	91·10	105·29	2·1931	1·1903	1·6990
August 1 ..	96·37	92·28	95·92	2·4679	1·5250	1·9800
,, 2 ..	92·08	89·48	92·06	2·6034	1·8751	—

	1	*2*	*3*	
a_1	−1·983	−2·608	−3·606	Regressions of cell width (Y) on days (X)
a_0	103·199	101·472	111·628	
a_1	0·21673	0·30495	0·32854	Regressions of log numbers (Y) on days (X)
a_0	1·55931	0·31213	0·67620	

	1	*2*	*3*
Cell width decrease/day (from regressions)	1·983	2·608	3·606
Log population increase/day	0·2167	0·3050	0·3285
Cell width decrease / Log population increase ..	9·151	8·551	10·977
Cell width decrease/division	2·754	2·574	3·304
Mean cell width	97·25	93·65	100·81
Cell width decrease/division in μ	1·24	1·16	1·49
Cell width in μ	43·76	42·14	45·36

1 eyepiece unit = 0·45μ

As a precaution, a third experimental series was carried out on the variation of cell w
Sceletonema costatum in culture media diluted with various quantities of distilled water;
if small variations in salinity could induce changes in cell width, then the method of estima
number of divisions by this method would be valueless. Nine cultures (S1–S9) and a contr
set up in 30 ml. wide-mouthed culture flasks. Measurements of 50 cells from each culture
control were made as often as possible between 26th June and 6th July, 1949. The dilut
each culture were as follows: S_1: 0·5 ml.; S_2: 1·0 ml.; S_3: 1·5 ml.; S_4: 2·0 ml.; S_5: 2·5 m
3·75 ml.; S_7: 5·0 ml.; S_8: 7·5 ml.; S_9: 10·0 ml. distilled water added to 20 ml. of Erdsc
Preliminary experiments with small dilutions, e.g., 0·1 ml. distilled water in 30 ml. Erdsc
had produced no measurable effect. The results of this series of experiments is shown in

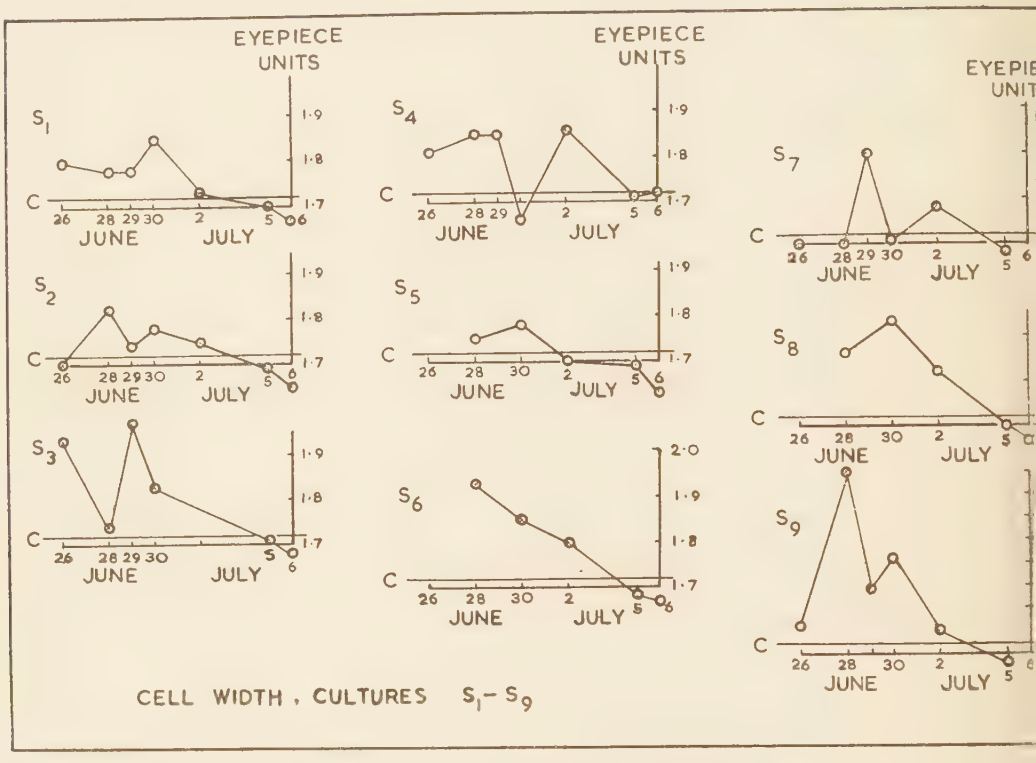


FIG. 28. THE CHANGE OF CELL WIDTH AT DIFFERENT LEVELS OF SALINITY
S_1, 0·5 ml.; S_2, 1·0 ml.; S_3, 1·5 ml.; S_4, 2·0 ml.; S_5, 2·5 ml.; S_6, 3·75 ml.; S_7, 5 ml.; S_8, 7·5 ml.; S_9, distilled water in 20 ml. Erdschreiber.

the control line marked C shown in each diagram indicates the cell width of the paren
from which all dilution cultures and the control were taken. The cell widths of the contro
did not rise above this line. It is clear from the figure that marked increases in cell wi
place; it is also clear that the maximum cell width was not reached until between 2 an
after the experiment started (it started on the 25th July and the first measurements were
the 26th). Estimations of growth-rate in numbers were made and these showed that one
took place every 3 or 4 days (the range was 3–5 days). As the cell lengths were maxima
26th July, it seems reasonable to assume that in diluted media, the cells took up water,
in length and then only extended in width when division took place. This would account
maxima in cell lengths that took place and late maxima in cell width. When the wate
situation has been adjusted by these means, the cell width (after the first division) tends to
A similar experiment on *Biddulphia sinensis* showed no variation in cell width but a marked
in cell length due to water uptake. It is quite possible that the effect was one of water up
affected the cell width after the first division. In the sea, the small variations in salinity
might find would be adjusted by variations in cell length only. The smallest dilution in th
ment is much larger than might be expected in the area under survey.

)m this survey of the experimental series, the following conclusions may be drawn : that a decrease in cell width takes place at each division in *Sceletonema costatum* and in *Biddulphia sinensis*;

that there is probably no effect of salinity in the Shields area upon this phenomenon. Similarly it is unlikely that temperature has a direct effect upon the phenomenon because the same effect was obtained whether the temperature was constant or variable. (Compare the results of the experiments on *Biddulphia* at constant temperature with those on *Sceletonema* under variable temperature conditions.)

ISTRIBUTIONS OF CELL WIDTHS FOR CRUISES VI, VII AND VIII AND THE DECREASE IN CELL WIDTH BETWEEN CRUISES

: experimental work described above finds its use in the diatom cell width distributions d from the sea samples. Diatoms from Cruises VI–VIII were measured across their transapical vith a phase contrast microscope (using a $\frac{1}{6}$, $\frac{1}{3}$ or $\frac{2}{3}$ objective). This microscope has the tage that the edges of the diatoms become very clear indeed; then the accuracy of a screw meter may be fully used. Measurements of as many diatoms as possible were made from ine Net samples. In the first two cruises (VI and VII), diatoms were plentiful and neasured at as many stations as possible; 50 of each species were measured at each station As the " A " group of patches of *Calanus* occupy most of the area of Cruises VI and VII, ll width distributions were made up of many observations. In Cruise VIII, the area of the group is a little smaller and the diatoms are much more thinly distributed and consequently are fewer observations. It will be remembered that it was argued that as these observations ken from the same water mass, identified from cruise to cruise by use of the copepods, it is able to assume that they are taken from the same populations. Thus, distributions from sive cruises should show similar component populations. The cell width distributions are : polymodal, and these were split into their components by a form of probit analysis. The of probit analysis used here is subject to two reservations. There is a subjective element in ection of the point at which to make the separation between populations; the use of the χ^2 limited as a test of goodness of fit for polymodal populations because of the wastage of s of freedom, consequently there is no adequate measure of the overall error of the method. cell width distributions have the following characters. Large cells are those that have just bored and small ones are those that are about to auxospore. A newly auxospored diatom a new series. So, the upper part of such a distribution consists of many numerically small tions. The lower part of the distribution consists of two or three numerically large popula- that have been dividing for a considerable period. We find, in fact that there are the 2 or 3 populations in the lower part of the distribution, which are interesting, and many trivial tions in the upper part. On the arithmetical probability paper used in this form of probit is, a line was drawn through these small populations in order to estimate the goodness of he more numerous populations of smaller diatoms.

e XXVII gives the means and standard deviations of populations of eight diatoms for s VI, VII and VIII. Seeing that the identity of populations between cruises is not in doubt been made by the identities of the " A " group of *Calanus* patches), the differences between cruises can only be the consequences of division and auxosporing. The observations on *ceras compressus* are straightforward, in that a decrease in cell size takes place in every tion. Those on *Thalassiosira* " *gravida* " are a little more complex: an auxosporing popula- ould be expected to produce in a period of time a population that is larger in size. A corollary would be that the smallest population becomes reduced in numbers as its auxospores join gest population. The largest population in Cruise VII is derived from the smallest-sized tion in Cruise VI. The same process appears to have taken place in *Rhizosolenia hebetata*, *nella japonica* and *Lauderia borealis*; the observations on *Chaetoceras* " *densus* " are com- to those on *Chaetoceras compressus*, that is division without auxosporing.

decrease in sizes of diatoms finds its use in the estimation of the number of divisions as ted above in cultures. Unfortunately, one cannot always set out to culture the diatom that nts. Again the diatoms off Northumberland in April and May 1949 were not cultured, and sults from culture of one species in one region or season might not agree with those from . For this reason, an attempt was made to make a direct estimate of the number of divisions

taking place between cruises by measuring the diatom cell wall widths of the material foun area; then, the mean decrease in cell width, divided by the cell wall width gives an estimat number of divisions that took place.

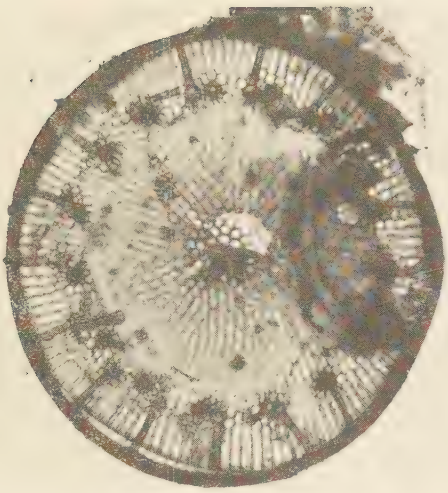
In Table XXVII, the decrease in cell size is shown in eyepiece units; the end column sh decrease in μ for each diatom. In the next section it will be shown how cell wall widt measured using an electron microscope, and how the estimate of the number of divisi derived.

Table XXVII

Decrease in cell width in μ of eight common diatoms between Cruises VI and VIII

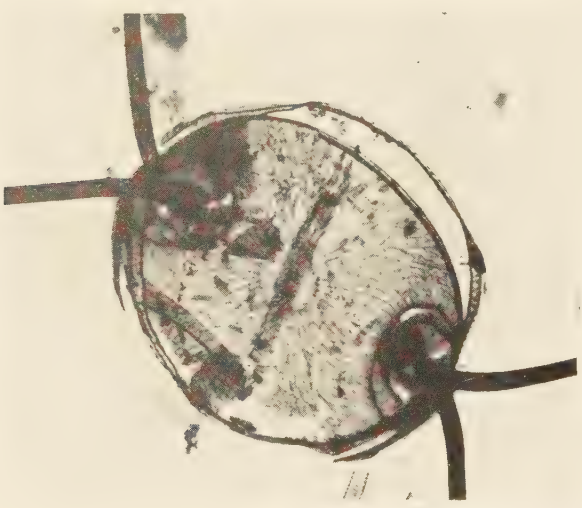
Species	*Cell sizes in e.u.*			*Decrease in cell size in e.u.*		*e.u. factor*	*Decr cell s*
	Cruise VI mean S.D.	*VII* mean S.D.	*VIII* mean S.D.	*VI-VII*	*VII-VIII*		*VI-VII*
Rhizosolenia hebetata ..	31·0 ± 3·0						
VI VII VIII	38·6 ± 2·3	32·5 ± 3·5	25·5 ± 4·0	6·1	7·0		2·77
pχ² 0·6 0·3 0·5	46·0 ± 3·5	39·5 ± 2·5	33·5 ± 3·5	6·5	6·0	(0·44)	
		47·2 ± 3·3	44·5 ± 3·0		2·7		
Ditylum Brightwellii ..	35·5 ± 3·0	34·0 ± 4·0	26·0 ± 3·5	1·5	8·0		3·78
VI VII VIII	43·7 ± 6·4	41·0 ± 3·5	36·5 ± 4·5	2·7	4·5	(1·8)	
pχ² 0·04 0·5		50·5 ± 2·0	49·5 ± 5·0		1·0		
		66·0 ± 10·0					
Asterionella japonica ..	177·5 ± 18·0						
VI VII VIII	225·0 ± 25·0	187·5 ± 25·0	153·0 ± 26·0	37·5	34·5	(0·22)	9·08
pχ² 0·2 0·3 0·1	280·0 ± 25·0	235·0 ± 15·0		45·0			
		287·5 ± 22·5	230·0 ± 23·0		57·5		
			285·0 ± 28·0				
Chaetoceras "densus" ..	91·0 ± 9·0	75·0 ± 12·0		16·0			
(includes *borealis*) ..	125·0 ± 24·0	98·0 ± 8·0		27·0		(0·44)	11·77
VI VII VIII		129·0 ± 12·0	100·0 ± 12·0		29·0		
pχ² 0·01 0·3	201·0 ± 28·0	164·0 ± 21·0	139·0 ± 11·0	37·0	25·0		
			188·0 ± 13·0				
Thalassiosira "gravida" ..	88·0 ± 6·5						
(includes *nordenskiöldii*)	117·0 ± 12·0	102·0 ± 10·0	98·0 ± 9·0	15·0	4·0		3·3
VI VII VIII	149·0 ± 29·0	118·5 ± 4·5		30·5		(0·22)	6·7
pχ² 0·4 0·02 0·02		133·0 ± 4·0	127·5 ± 15·0		5·5		
		164·0 ± 17·0	164·0 ± 17·5				
Lauderia borealis	148·0 ± 3·5						
VI VII VIII	171·0 ± 8·5	167·0 ± 14·0	163·0 ± 10·5	4·0	4·0	(0·22)	0·8
pχ² 0·8 0·08 0·02	198·0 ± 8·2	201·0 ± 10·0	190·0 ± 7·5		11·0		
			239·5 ± 15·0				
Chaetoceras compressus ..	49·0 ± 7·5	40·0 ± 4·0		9·0			2·9
VI VII VIII	65·0 ± 7·0	48·5 ± 4·5	47·0 ± 7·0	16·5	1·5	(0·22)	
pχ² 0·03 0·01 0·05	80·5 ± 13·0	71·5 ± 7·0	61·0 ± 7·5	9·0	10·5		
			81·5 ± 11·5				
Sceletonema costatum ..	25·5 ± 2·5	19·8 ± 3·5	16·5	5·7	3·3		3·7
VI VII	33·5 ± 2·5	31·5 ± 1·25		2·0		(0·91)	
No test made ..	44·0 ± 8·0	39·5 ± 1·0		4·5			
		55·2 ± 1·5					

(χ² is a measure of the goodness of fit of the distribution calculated from the given means and standard deviations to the observations)



Thalassiosira nordenskiöldii

Chaetoceras compressus

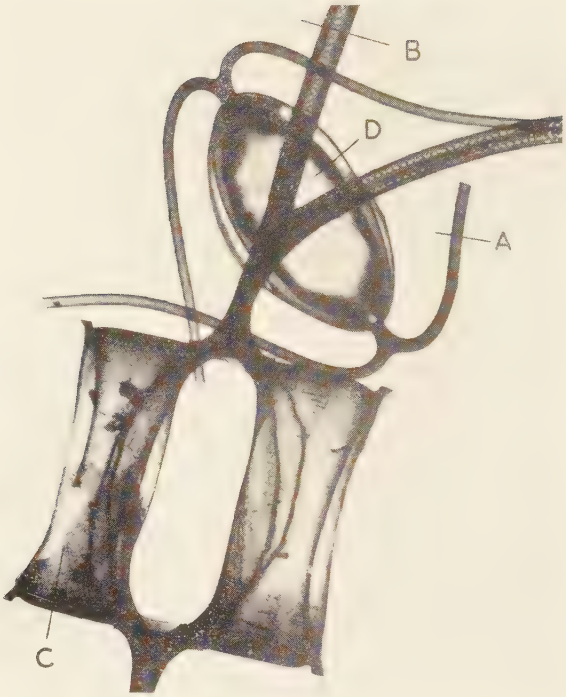


Chaetoceras compressus

ELECTRON PHOTOMICROGRAPHS OF TWO DIATOMS, SHOWING THE VALVE FROM AN END-ON VIEW

In each photograph, the cell wall thickness is shown in section.

PLATE I



ELECTRON PHOTOMICROGRAPH OF *Chaetoceras decipiens* AND A RESTING SPORE OF *Chaetoceras cinctus*

This shows the possible measurement that one might take to obtain the cell wall thickness:

(*a*) spine in the end-on view,

(*b*) spine in the lateral view,

(*c*) wall in the lateral view,

(*d*) wall in the end-on view. This, the radial measurement, was chosen. (Phillips m 4,050, 60 kv, taken by Mr. Ripley of the Biophysics Sub-department, D of Botany, Leeds University).

PLATE II

vas then decided to try to measure the thickness of the cell wall with the use of the electron scope. Diatoms have been used as test objects for both light and electron microscopy; is workers have published electron photomicrographs of diatoms (Krause, 1936; Kolbe Jölz, 1943; Mühlethaler and Braun, 1946; Kolbe, 1948), but these studies were in general ed to the form of the wall structure, rather than to its thickness.

fessor R. D. Preston, F.R.S., has allowed me to use his electron microscope (Phillips, up to 0,000 and 80 kv.); Mr. Kuyper and Mr. Ripley of the Biophysics Sub-department of the rtment of Botany, University of Leeds, taught me how to use the instrument, taught me the ique of mounting the diatoms on the grids, took the photographs and developed them for me.

itoms from the station samples in the " A " group of patches were mixed, concentrated and, as possible, they were separated into species by the use of a centrifuge. These were washed tilled water, to get rid of the salt; they were then warmed gently in sulphuric acid. Boiling ncentrated acid certainly cleaned the valves and reduced the organic matter, but it often broke alves, especially those of the thin-walled *Chaetoceras compressus*; subsequently the frustules warmed gently in 50 per cent acid. After the acid treatment, the diatom valves, now separated, washed again in distilled water until there was no trace of acid. These were then mounted ids covered with *formvar* membranes, by means of a platinum loop. As they were often ated by the acid treatment, the valves of many of the diatoms were allowed to fall flat on their zones on the grid. This means that the thickness of the cell wall is across the beam of the ons. As silica is opaque to the electron beam, the thickness of the cell wall appears black on hotograph.

te I shows the end-on view of the valves of *Thalassiosira nordenskiöldii* and *Chaetoceras com-s*. The *Thalassiosira* frustule shows the cell wall quite clearly; the variations in thickness to be partly due to electron shadows because the valve has settled slightly at an angle to the on beam. This is shown most clearly on the top right-hand side of the picture of *Thalassiosira vida* "; apart from this, there is a certain amount of variation in the wall itself, but this is not great. The *Chaetoceras* frustule shows in the same way the constant thickness of the cell wall; ilar thickness surrounds a " well " from which the spines spring. The siliceous structure in pecies is quite different; rather than being regular and well defined, the network is irregularly and a little diffuse. In both cases there is a certain amount of dark material which is almost nly the remains of organic material.

te II shows a photograph of *Chaetoceras decipiens* and of a resting spore of *Chaetoceras s* giving the three possible measurements that might be used—the radial cell wall thickness own in Fig. 29, the thickness of the spine wall and the thickness of the wall seen from the side cell. It is clear that there is a marked difference between the thickness of the spine wall and ickness of the wall seen from the side of the cell. These measurements show no difference

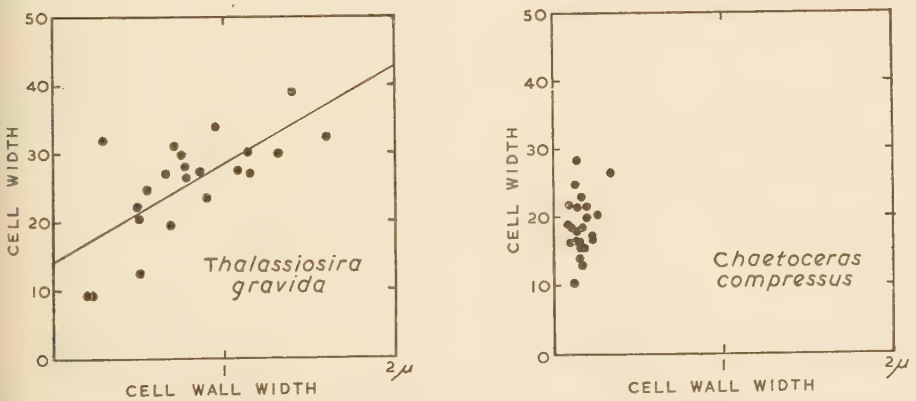


FIG. 29. RELATION BETWEEN CELL WIDTH AND CELL WALL THICKNESS IN *Thalassiosira gravida* AND *Chaetoceras compressus*
Cell width and cell wall thickness are both measured in μ.

between the radial measurements and the spinal measurements. However, the spines do not appear clearly enough to give a consistent measurement; in the case of *Chaetoceras compre* spines are always nearly opaque. This figure shows again that the radial measurements a consistent.

A number of measurements were made on *Thalassiosira* " *gravida* " and *Chaetoceras com* These are plotted as cell wall thickness against cell width in Fig. 29. Two points are imm obvious; that there is a regression in the case of *Thalassiosira* " *gravida* " but not in that of *ceras compressus*. The cell walls of *Chaetoceras compressus* are considerably less thick tha of *Thalassiosira* " *gravida* ". It is probable that the regression of cell wall thickness on ce for *Thalassiosira* is a curvilinear one; there is no immediate theoretical reason why the c should become increasingly thicker with size, unless it be the mechanical explanation tha wise the cell would then be weaker. However, a great number of observations would be n to find whether the residual variance from a possible curvilinear relation was significantly l that from a linear regression.

Table XXVIII gives the characters of the regressions for *Sceletonema costatum*, *Thalc* " *gravida* " (which includes *nordenskiöldii*), *Chaetoceras* " *densus* " (which includes " *bo* and *Chaetoceras compressus*.

Table XXVIII

Regressions between cell width and cell wall width for four diatoms

Species	a_0	a_1	*P*	*Significant or not Significant*
Sceletonema costatum ..	5·14	5·71	0·05	S.
Thalassiosira " *gravida* "	14·26	14·24	< 0·01	S.
Chaetoceras " *densus* " ..	53·74	−0·91	> 0·9	Not S.
Chaetoceras compressus	15·98	17·58	0·3	Not S.

Thus it appears that the chaetocerid cell walls remain constant in width, whereas the c of *Thalassiosira* and *Sceletonema* become thinner as the cell becomes smaller.

There is the possibility that the cell wall decrease per division is larger than the width of wall; this would be so if there was a good gap between the walls. Then, one would expect cell wall width as estimated by culture methods would be larger than the cell wall width as directly; but there is no significant difference between the three culture estimates and the microscope measurements of the cell wall of *Sceletonema costatum*, the only species of t successfully cultured.

Table XXIX

Derivation of the number of divisions of eight diatom species between Cruise VI and Cruise VIII

Species	*Decrease in cell width in μ from Table XXVII*		*Cell wall width in μ*	*Divisions*		*Divisio per*
	VI-VII	*VII-VIII*		*VI-VII*	*VII-VIII*	*VI-VII*
Rhizosolenia hebetata	2·77	2·30	0·6	4·62	3·84	0·355
Ditylum Brightwellii	3·78	8·10	0·7	5·40	11·57	0·415
Asterionella japonica	9·08	10·12	0·24	37·83	42·17	2·910
Chaetoceras " *densus* "	11·73	11·88	1·05	11·16	11·30	0·858
Thalassiosira " *gravida* " ..	3·30	0·88	0·7; 0·54	4·71	1·63	0·422
	6·71	1·21	1·07; 1·00	6·27	1·21	
Chaetoceras compressus ..	2·53	1·32	0·17	14·88	7·76	1·145
Lauderia borealis	0·88	1·65	0·7	1·26	2·36	0·097
Sceletonema costatum	3·70	3·00	0·5	7·40	6·00	0·569

Note. The cell wall width of *Rhizosolenia hebetata*, *Ditylum Brightwellii* and *Lauderia borealis* were indirectly from broken material; the results were not entirely satisfactory, but the estimate of cell wall wi likely to be more than 30–50 per cent wrong.

derivation of the division rates per day from the cell width decrease and the cell wall width wn in Table XXIX. The number of divisions is estimated by dividing the decrease in cell by the cell wall width. These estimates are derived from the actual material from Cruises VI, id VIII, as given in Table XXVII.

3. Estimation of the " Natural " Mortality of Diatoms

en the reproductive rate of the diatoms, their counted numbers at intervals of time, and the er (and rate of change of numbers) of herbivores between these intervals, their mortality may imated. Mortality of plants may be attributed to two types of cause: (*a*) death by herbivore ig, and (*b*) death by non-grazing factors. This second type of mortality can be recognized e presence of complete and empty frustules, and counts of complete and empty frustules will o a minimal estimate of this type of mortality. This mortality, I have called " natural lity," from an analogy with fish population studies. I have noticed that this effect is very ed during the autumn outburst of *Rhizosolenia styliformis* and *Biddulphia sinensis* off East a; as many as 80 per cent of the cells were complete and empty in 1947. This observation is ly complementary to that of Savage and Wimpenny (1936) that the population of *Rhizosolenia rmis* suddenly disappeared in 1934 as if a mortality had suddenly become effective. In the the cause of natural mortality most likely to be suggested would be nutrient depletion. ver, the cause is equally likely to be due to turbulence, for this limits the possible quantity of ion obtainable.

ie dynamics of the plant populations are analogous to those of the fish populations. One ates the natural mortality of a fish species, having estimated the fishing mortality and total lity; it is hoped to estimate the grazing mortality of the diatoms, having estimated the total lity and natural mortality. As the diatoms were being counted, counts of dead and empty ken frustules were also made. These counts expressed as numbers beneath 1/100m.^{2} were d on charts at the appropriate stations and the charts were contoured and planimetered scribed in Part II. The results are shown for the " A " and " B " groups of patches in XXX. The numbers given in the table multiplied by $6{\cdot}4 \times 10^{15}$ give estimates of the actual ation numbers. It will be noted that there is no estimate for Cruise VIII, in which the numbers e cells were small.

Table XXX

Numbers of dead cells in area units in Cruises VI and VII

Species	*Cruise VI*		*Cruise VII*	
	" A " Group	*" B " Group*	*" A " Group*	*" B " Group*
Asterionella japonica ..	4·5	—	0·7	—
Chaetoceras brevis ..	54·3	—	26·0	—
Chaetoceras compressus	7·5	—	—	—
Cerataulina bergoni ..	—	—	—	1·4
Ditylum Brightwellii ..	46·5	—	4·9	—
Lauderia borealis ..	37·8	170·6	30·0	—
Rhizosolenia hebetata ..	—	—	—	1·9
Sceletonema costatum ..	51·1	—	4·8	—
Thalassiosira " gravida "	12,293·8	122·5	244·5	3·5

(*These figures should be multiplied by* $6{\cdot}4 \times 10^{15}$ *to give estimates of actual numbers*)

eeds no emphasizing that the method can only apply to the diatoms. As dinoflagellates much less important, and as it was thought that the μ-flagellates were also less important, stimate is probably fairly complete.

ight well be argued that this estimate is vitiated by the sinking of the diatom frustules. There tle evidence on the rate at which diatom frustules sink. Apstein (1910) showed that preserved ns sink at rates varying between 3 and 40 mm./minute; Gross and Zeuthen (1948) have shown he resting spores of *Ditylum Brightwellii* sink 4–6 mm./minute. It is therefore reasonable to ie that diatom frustules sink at a speed of 10 m. in 24 hours, disregarding vertical turbulence.

This means that they would reach the bottom in about 5 days, an estimate that will be us later stage.

In Part II various estimates of the volumes of diatoms are given in μ^3. These estima another use in making estimates of total plant volume. The numbers of each species are mu by the mean volume of that species in μ^3 to give a total volume. This procedure is carried as many plants as possible and estimates of the total plant volume are made. This can carried out on the estimates of dead cells. Table XXXI gives the total plant volume in μ and dead for the " A " group of patches in Cruises VI, VII and VIII. It will be noted t proportion of dead cells to live cells is one-fifth in Cruise VI and that this proportion is r to one-twentieth in Cruise VII. This is a most interesting observation because the nutrie in Cruise VII is 3·95 μgP/l less than in Cruise VI (" A " patch); thus the proportion of de decreases as the nutrient level decreases. The implication is that the mortality is not rel nutrient depletion, but to some other factor, probably turbulence.

Table XXXI

Total plant volume in the " A " group of patches in μ^3 dead and alive

	Dead	*Alive*
Cruise VI	$9{\cdot}8496 \times 10^{23}$	$4{\cdot}5675 \times 10^{24}$
Cruise VII	$3{\cdot}3082 \times 10^{22}$	$6{\cdot}6197 \times 10^{23}$
Cruise VIII	—	$2{\cdot}8188 \times 10^{22}$

4. Estimation of Production

In any estimate of plant production in the sea, it is necessary to know the division rate diatoms (or the mean production increase coefficient, to use Riley's term), their natural m rates and the numbers in the same water mass at different times. In this estimate it will be a that any loss in numbers between cruises that is not accounted for in terms of reproduct and " natural mortality " is due to herbivore grazing. Because division rates and " n mortality rates were estimated for each common diatom species, the following equation h applied for each species:

$$\frac{dP}{dt} = -K.P + (R-M)P \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad ..$$

Where P is the number of a diatom species

R is the daily division rate of the diatom species

M is the daily " natural " mortality rate of the diatom species

K is the daily herbivore grazing rate on the diatom species.

Integrating this equation and applying it to any two cruises on the same water mass,

$$P_1 = P_0 e^{(R-M-K)t} \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad ..$$

where P_0 is the number of a diatom species in the first cruise

P_1 is the number of a diatom species in the second cruise

t is the time between cruises in days.

The daily rate of herbivore grazing may be estimated in the following way:

$$K = \frac{(R-M)t - \log \frac{P_1}{P_0}}{t} \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad ..$$

It must be pointed out that, to simplify the working at this stage, it was assumed that the r of herbivores remained constant between cruises; so, no factor was used to deal with any he increase, between cruises.

The " natural " mortality rate is found by an approximation. The numbers of comp empty cells were expressed as percentages of the numbers of live cells (%M). It was assun

diatoms sink to the bottom in five days, so a value of %M found on any day is the result of ural" mortality for the previous five days.

en, the "natural" mortality between t = − 5 and t = 0 is,

$$\frac{P_0M}{R-M-K}\left\{1 - e^{(-5)(R-M-K)}\right\} = \% \, M.P_0,$$

$$\% \, M = \frac{(1-e^{-5(R-M-K)})\, M}{R-M-K} \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad (4)$$

R−M−K is small,

$$\% \, M = \frac{5\,(R-M-K)\, M}{R-M-K} = 5M \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad (5)$$

M is small compared with (R−K)

$$\% \, M = -M\left\{\frac{e^{-5(R-K)}-1}{R-K}\right\} \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad (6)$$

ing an estimated figure from (6) for M, M′, put M = M′ + M″ where M″ is small;

ien,

$$\% \, M = -(M' + M'')\left\{\frac{e^{-5(R-M'-K)} - 1}{R - M' - K}\right\} \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad .. \quad (7)$$

M was always small compared with (R − K), M was estimated from (6) and (7).

oduction is defined as the number of cells produced in a given time, then the production in time dt = P.Rdt

ow, we know that $P = P_0 e^{(R-M-K)t}$

otal production is

$$\int_0^t P_0.e^{(R-M-K)t}.R\,dt$$

$$= P_0R\left[\frac{e^{(R-M-K)t}}{R-M-K}\right]_0^t$$

$$= P_0.R\left\{\frac{e^{(R-M-K)t}-1}{R-M-K}\right\}$$

ie "natural" mortality of a diatom species between two cruises is:

$$\frac{P_0M}{R-M-K}\left\{e^{(R-M-K)t}-1\right\}$$

ie number of a diatom species grazed (the number of cells eaten) between two cruises is:

$$\frac{P_0K}{R-M-K}\left\{e^{(R-M-K)t}-1\right\}$$

is assumed, in these three estimates, that the three rates, R, M and K are constant between wo cruises.

ese three quantities, production, "natural" mortality and number grazed, were estimated ine diatoms in the "A" group of patches, between Cruises VI–VII and VII–VIII. The cell mes of these diatoms are known and so each of the above quantities may be reduced to plant me in μ^3 of plant material. Estimates of production, natural mortality and grazing mortality wo periods, Cruises VI–VII and Cruises VII–VIII are set out in Table XXXII. Division rates *Asterionella japonica*, *Chaetoceras brevis*, *Chaetoceras compressus*, *Chaetoceras densus*, *assiosira gravida* and *Sceletonema costatum* were worked out by the methods given above in on 2. For *Lauderia borealis*, *Rhizosolenia hebetata* and *Ditylum Brightwellii*, divisions were ned from the estimated cell size decrease and an estimate of the cell wall thickness.

though this estimate of diatom production is not complete, it is thought that this estimate unts for at least 70 per cent of the production taking place. It is interesting to notice that ough the smaller diatoms are much more numerous than larger ones, *Lauderia borealis* is hird largest producer in terms of production and cell volume. The volume eaten is greater the volume produced because it includes a proportion of the standing crop at the start of the od.

Table XXXII

Production of diatoms, Cruises VI–VIII, " A " group of patches

Species	*Production (numbers)*	*" Natural mortality " (numbers)*	*Numbers of plants eaten*	*Cell volumes in μ^3*	*Product cell vo in μ*
Asterionella japonica					
VI–VII	$5{\cdot}14 \times 10^{21}$	$3{\cdot}36 \times 10^{16}$	$5{\cdot}27 \times 10^{21}$	821	4,224 ×
VII–VIII	$6{\cdot}99 \times 10^{20}$	$2{\cdot}54 \times 10^{15}$	$7{\cdot}82 \times 10^{20}$	821	574 ×
Chaetoceras brevis					
VI–VII	$3{\cdot}96 \times 10^{20}$	$7{\cdot}54 \times 10^{17}$	$3{\cdot}76 \times 10^{20}$	1,584	627 ×
VII–VIII	$6{\cdot}72 \times 10^{19}$	$1{\cdot}39 \times 10^{17}$	$1{\cdot}02 \times 10^{20}$	1,584	106 ×
Chaetoceras compressus					
VI–VII	$1{\cdot}80 \times 10^{21}$	—	$1{\cdot}80 \times 10^{21}$	1,584	2,847 ×
VII–VIII	$9{\cdot}86 \times 10^{19}$	—	$2{\cdot}18 \times 10^{20}$	1,584	156 ×
Chaetoceras " densus "					
VI–VII	$7{\cdot}31 \times 10^{17}$	—	$9{\cdot}15 \times 10^{17}$	18,407	13·5 ×
VII–VIII	$1{\cdot}24 \times 10^{17}$	—	$1{\cdot}25 \times 10^{17}$	18,407	2·27 ×
Lauderia borealis					
VI–VII	$5{\cdot}70 \times 10^{18}$	$1{\cdot}69 \times 10^{17}$	$1{\cdot}95 \times 10^{19}$	49,232	281 ×
VII–VIII	$3{\cdot}71 \times 10^{17}$	$9{\cdot}75 \times 10^{16}$	$9{\cdot}34 \times 10^{17}$	49,232	18·3 ×
Rhizosolenia hebetata					
VI–VII	$9{\cdot}14 \times 10^{17}$	—	$9{\cdot}55 \times 10^{17}$	13,403	12·3 ×
VII–VIII	$2{\cdot}25 \times 10^{17}$	—	$3{\cdot}93 \times 10^{17}$	13,403	3·01 ×
Thalassiosira " gravida "					
VI–VII	$2{\cdot}75 \times 10^{20}$	$1{\cdot}13 \times 10^{19}$	$5{\cdot}02 \times 10^{20}$	11,768	3,236 ×
VII–VIII	$5{\cdot}52 \times 10^{17}$	$3{\cdot}26 \times 10^{17}$	$2{\cdot}29 \times 10^{18}$	11,768	6·50 ×
Sceletonema costatum					
VI–VII	$1{\cdot}67 \times 10^{20}$	$3{\cdot}54 \times 10^{17}$	$1{\cdot}88 \times 10^{20}$	200	33·5 ×
VII–VIII	$2{\cdot}34 \times 10^{19}$	$3{\cdot}42 \times 10^{16}$	$3{\cdot}64 \times 10^{19}$	200	4·68 ×
Ditylum Brightwellii					
VI–VII	$1{\cdot}08 \times 10^{19}$	$2{\cdot}88 \times 10^{17}$	$1{\cdot}28 \times 10^{19}$	156,002	1,692 ×
VII–VIII	$2{\cdot}65 \times 10^{18}$	$1{\cdot}98 \times 10^{16}$	$3{\cdot}70 \times 10^{18}$	156,002	413 ×

VI–VII ..	Total production	$12{,}966 \times 10^{21}\mu^3$
	Total " natural " mortality ..	$187{\cdot}95 \times 10^{21}\mu^3$
	Total volume eaten	$16{,}705 \times 10^{21}\mu^3$
VII–VIII ..	Total production	$1{,}284 \times 10^{21}\mu^3$
	Total " natural " mortality ..	$11{\cdot}96 \times 10^{21}\mu^3$
	Total volume eaten	$1{,}815 \times 10^{21}\mu^3$

Such estimates of production are useful in two ways: (*a*) in relation to the herbivores relation to the nutrients. The latter will be left till the next section. From comparison quantity eaten and that lost by natural mortality with the quantity produced (Table X about 90 per cent of the diatoms produced are being eaten. They are being eaten by the a and it is possible to find out which animals are responsible for the greater part of the grazin

It was first necessary to separate the proportions of the production taken by the *Calanus* p tions on the one hand and by their competitors on the other. This was done in the followi

Measurements in length were made of each adult and copepodite stage of Calanus, ♂, juvenile, *Pseudo-calanus elongatus*, ♂, ♀ and juvenile, *Paracalanus parvus*, and *Temora long* Fifty specimens of each group were measured for each of the three Cruises VI–VIII. The of these measurements of each group were cubed to give an expression proportionate to it volume. The numbers caught beneath 1m.^{2} were then multiplied by the volume factors. transformed numbers were plotted at each station on the cruise charts; the charts were cor and the resulting patches were planimetered to give estimates of the transformed numbers group of patches. These estimates of comparative *grazing capacity* of *Calanus* copepodite and " non-calanids " are given in Table XXXIII; it is interesting to notice that the *grazing c* of the " non-calanids " becomes greater in Cruise VIII. Thus it is possible that the reduc recruitment of *Calanus* stage I in later cruises is related partly to the increased *grazing c* of the " non-calanids ".

Table XXXIII

mbers of each *Calanus* stage and each "*non-calanid*" group multiplied by their volume factors and added as *Calanus* and "*non-calanid*"

	Calanus stages	"*Non-calanids*"
Cruise VI	115,939,000	33,738,000
Cruise VII	115,366,000	50,865,000
Cruise VIII	103,607,000	153,410,000

mparing the estimated grazing capacity of *Calanus* stages and non-calanids, we may conclude *Calanus* took over 70 per cent of the numbers of diatoms eaten between Cruises VI and VII e "A" group of patches (means of grazing capacities for the two cruises were used). The vations allow calculation of the proportionate grazing capacity for each copepodite stage *alanus*. The 70 per cent of the total grazed production in plant volume ($1{\cdot}297 \times 10^{25}\ \mu^3$) is up in the proportions shown in Table XXXIV, where the quantity of material eaten by each al per day is also shown as worked out from the numbers of each stage. It must be pointed hat the quantities of food taken by *Calanus* stages are somewhat over-estimated (by perhaps or three times), because the estimate of *Calanus* numbers does not include those eaten by tors.

Table XXXIV

Quantity of food taken by each copepodite stage of *Calanus* per day, Cruises VI–VII

	Copepodite stage					
	I	*II*	*III*	*IV*	*V*	*VI*
rtionate grazing acity	1·67%	5·45%	18·96%	27·16%	30·58%	16·18%
tities of plant μ^3 sumed	$1{\cdot}586 \times 10^{23}$	$5{\cdot}175 \times 10^{23}$	$1{\cdot}800 \times 10^{24}$	$2{\cdot}579 \times 10^{24}$	$2{\cdot}904 \times 10^{24}$	$1{\cdot}536 \times 10^{24}$
bers of each stage	$1{\cdot}633 \times 10^{14}$	$2{\cdot}269 \times 10^{14}$	$2{\cdot}293 \times 10^{14}$	$1{\cdot}190 \times 10^{14}$	$6{\cdot}592 \times 10^{13}$	$1{\cdot}820 \times 10^{13}$
μ^3/animal ..	$9{\cdot}709 \times 10^{8}$	$2{\cdot}281 \times 10^{9}$	$7{\cdot}852 \times 10^{9}$	$2{\cdot}167 \times 10^{10}$	$4{\cdot}405 \times 10^{10}$	$8{\cdot}441 \times 10^{10}$
μ^3/animal/day	$7{\cdot}469 \times 10^{7}$	$1{\cdot}755 \times 10^{8}$	$6{\cdot}040 \times 10^{8}$	$1{\cdot}667 \times 10^{9}$	$3{\cdot}388 \times 10^{9}$	$6{\cdot}493 \times 10^{9}$
mm^3/animal/day	0·07	0·17	0·60	1·67	3·39	6·49

similar estimate for Cruises VII–VIII was as follows:

	Copepodite stage					
	I	*II*	*III*	*IV*	*V*	*VI*
mm^3/animal/day ..	0·00	0·01	0·03	0·08	0·18	0·46

will be noticed that the quantity of food per *Calanus* is much reduced between Cruises VII–VIII mpared with the period between Cruises VI–VII. This is related to the fact that the production duced by ten times between the two periods.

is instructive to compare the grazing coefficients upon each diatom species in the two periods ined, shown in Table XXXV. It will be noticed that the daily grazing coefficients are com- ble in both periods; where the coefficient has become reduced, the standing crop has been ced, and where the coefficient has increased, the standing crop has been maintained. Hence, grazing has been transferred from the diatoms, the numbers of which have been reduced, to , the numbers of which have been maintained.

Table XXXV

Grazing coefficients K on nine common diatoms, for Cruises VI–VII and Cruises VII–VIII

Species	*VI–VII*	*VII–VIII*
Asterionella japonica	2·9779	2·7762
Chaetoceras brevis	1·0863	0·6933
Chaetoceras compressus	1·1463	1·0088
Chaetoceras "densus"	1·0745	0·6746
Lauderia borealis	0·3312	0·3499
Rhizosolenia hebetata	0·3713	0·3953
Thalassiosira "gravida"	0·7709	0·3482
Sceletonema costatum	0·6436	0·5416
Ditylum Brightwellii	0·4914	0·9514

(*From Equation 3*)

The quantities of food eaten by one *Calanus* imply a " volume swept clear " that is sixt greater than hitherto published estimates. Between Cruises VI and VII the standing cr reduced by six times. If the plants were not dividing at all, this reduction would be the e natural mortality and grazing mortality only, i.e.,

$e^{-(M+K)t} = 0{\cdot}16$ $\therefore (M+K)t = 1{\cdot}83$

$t = 13$, and ignoring M,

$K = 0{\cdot}14$

The number of *Calanus* stages on Cruise VI was 0·08/litre and the number of *non-Calanus* was 0·1/litre. Let us assume that *Calanus* is three times as effective as a *non-Calanus* in g it may be calculated that the " volume swept clear " per average *Calanus* stage is about 1 lit Riley, Stommel and Bumpus (1949) have summarized published estimates of *Calanus* s grazing and state *Calanus* stage V " sweeps clear " 70–100 ml. of water each day; this is cor by the later observations of Gauld (1951). Had the diatoms not been dividing, there wo a discrepancy of 10–15 times between my estimate and previous published ones; if the diato dividing at the estimated mean division rate of 0·402/day, then the discrepancy reaches 25–3 for *Calanus* stage V and 60 times for an average *Calanus* stage.

The estimate of the grazing coefficient depends on the observed decrease in numbers, estimated division rate and on the estimated natural mortality rate. If the discrepancy w only to a wrong estimate of the natural mortality rate, one would expect to find nine-tenths observed decrease in numbers on the bottom of the sea; this did not happen when Harvey *et al* examined this point. If the plants were not dividing at all, the experimental estimates of would be only about one-tenth of the observed. Hence, the discrepancy must lie betwe observed and experimental estimates of grazing.

Grazing by *Calanus* is likely to take place in two ways, by filtration and by food capture. (1951) has shown that the daily grazing coefficient of 1 *Calanus* stage V by filtration of *Chl monas* was 0·95. Harvey (1937) found that the daily grazing coefficient of 1 *Calanus* stage V with the size of the diatom (*Nitzschia* 0·01, *Lauderia* 0·126 and *Ditylum* 0·54). If it is assum *Calanus* captured and broke diatoms and filtered off the contents, then the process of grazin place in two stages—capture from random contacts and intermittent filtration. I have *Pseudocalanus* take a *Biddulphia sinensis* almost as big as itself, break it and filter off some contents.

Using the observed grazing coefficient, *Calanus* stage V would need to kill one diatom size of *Lauderia* every 8 seconds in order to sufficiently reduce the plant numbers; in Cr there were three " *Lauderia* "-sized diatoms in every cm. of linear movement. This sounds rea and a grazing coefficient attributable to killing diatoms by *Calanus* stage V of 1–2·5 is plau

5. Use of Phosphorus

The winter maximum of phosphate phosphorus has been shown to be an index of p productivity. The total quantity of phosphorus, including that in organic compounds, c be used as an index of potential productivity (Harvey). The importance of phosphorus because it is often a limiting nutrient to production.

On the assumption that there is a linear relation between quantity of phosphorus and q of phytoplankton, the total yearly phosphorus figures from Plymouth have been used to co phytoplankton growth curves that are in some years perfectly consistent. In other years, sig breaks in the curves occurred, indicating presumably a change in the water mass at the sa station. The detailed connection between phosphorus and plant production had not been further until the publication of Pratt's (1950) study of a fertilized salt water tank. Here sig correlations were obtained between the rate of phosphorus assimilation and the size of th standing crop. This follows clearly from the first relation, when it is realized that ther practically no herbivores in the tank.

Experiments were carried out at Lowestoft on the phosphorus uptake of diatoms at d temperatures. Experiments on *Phaeodactylum* were carried out under the conditions descr Part II. The results are summarized in Table IV, showing that the rate of phosphorus varied with temperature. This part of the experiment extended over the first 48 or 72 hours, which phosphorus was absorbed into the cells and during which growth did not significant

It is considered significant that in this form of experiment (described in more detail in
I) growth did not take place until all the phosphorus had been taken up. Hence, if large
ities of phosphorus were added, a fairly long lag phase was to be expected. When the results
ted to a growth curve (e.g., the logistic curve), this lag phase appears as an anomaly to the
A typical experiment is represented in Fig. 30. The experiment was continued until all
h had ceased, i.e., until an asymptotic value had been reached. Growth in numbers ceased
asymptote, presumably because the phosphorus taken up in the lag phase was now used up.

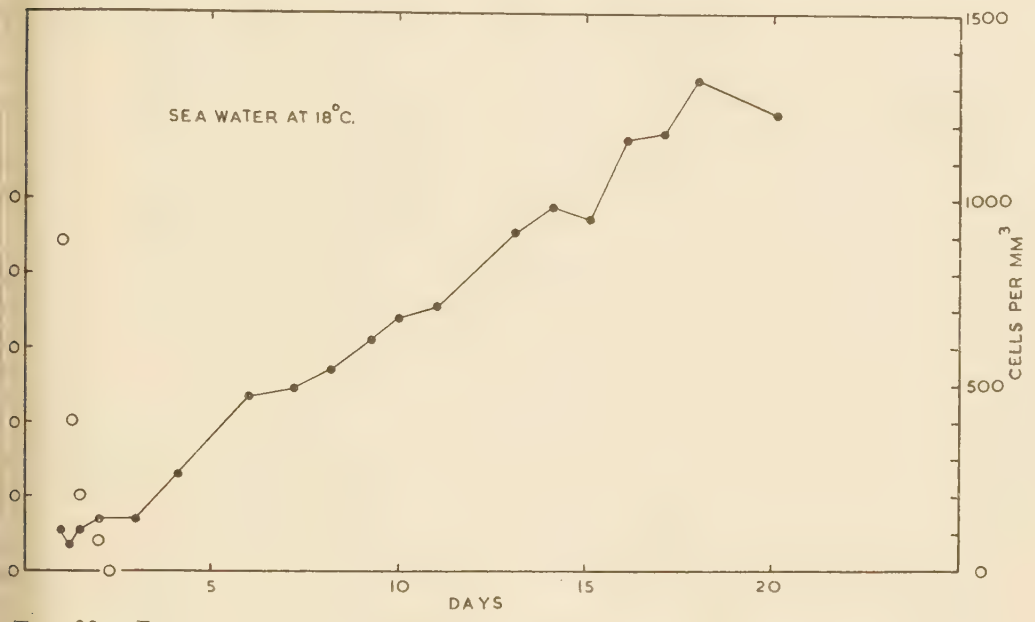


FIG. 30. RELATION BETWEEN PHOSPHORUS UPTAKE AND GROWTH IN NUMBERS OF *Phaeodactylum*

mples for phosphorus estimation were taken on the same culture in the first three days of the experiment.

results from these experiments were fitted by the logistic equation, because a marked
tote had been found. It was at once clear that the slopes of the lines differed markedly at
nt temperatures (see Fig. 31). The rate of phosphorus uptake was greatest at 10° C. and
nsiderably less at higher and lower temperatures (see Table IV). The experimental arrange-
s, of course, artificial and in the sea one would expect that growth and uptake would go on at
me time, if only because the differences in phosphorus concentration that one cell would
ıter are never so great as the quantities added in these experiments. If this is the marine
ɔn, then up to 10° C. both uptake and growth will increase with temperature, but above
uptake will limit growth, because it decreases with increasing temperature, whereas growth
es with increasing temperature. This, however, would be of little importance in the spring
elds because temperatures do not rise much above 10° C. It might well be of importance,
er, in the early autumn.

relation between phosphorus uptake and growth obtained was markedly curvilinear in these
nents in which there was no growth until all the phosphorus was used up, and for which,
re, phosphorus uptake is given by the initial quantity per cell before growth started (Fig. 34).
cond experiment was carried out on the extent of growth of *Phaeodactylum* at a constant
ature under different phosphorus concentrations. A medium analogous to Chu's sea-
medium was used in this experiment, as I wanted to be quite sure that there would be no
trace elements in the culture medium. The composition of the medium was altered in
espects—that no phosphorus was added and that nitrate nitrogen was added in excess and
iosphorus-free sea water was used as a basis; this is sea water from which phosphorus had
hausted by diatom growth. Herein lies the necessity of using this type of medium, because
possible that some trace elements would also be exhausted from the basic sea water at the

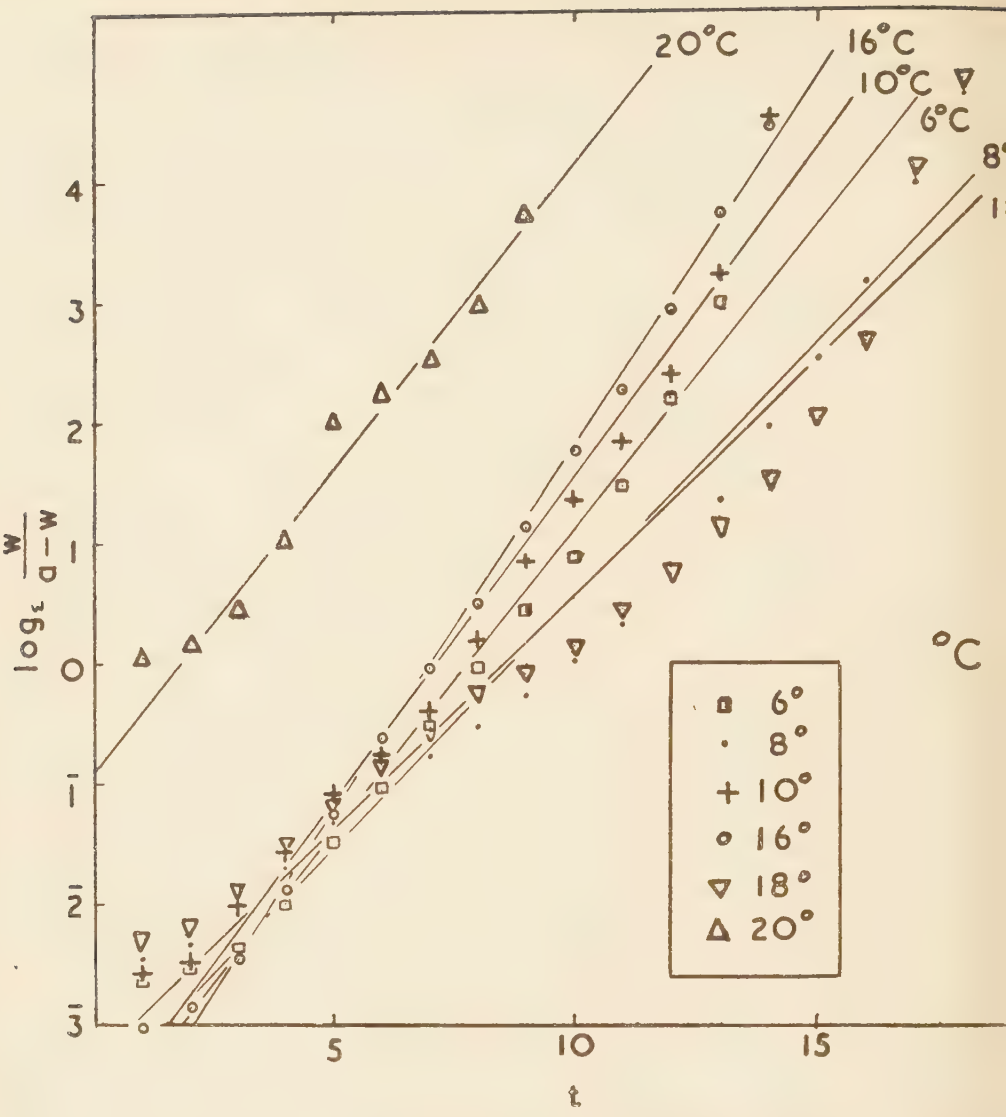


FIG. 31. THE RESULTS OF THE EXPERIMENT ON PHOSPHORUS UPTAKE AT DIFFERENT TEMPERATURES AT THE SAME PHOSPHORUS CONCENTRATION
The key, inset, gives the different temperatures for each set.

same time as the phosphorus. In this experiment, growth rates were roughly constant. shows the relation between the number of cells at each phosphorus concentration and ti very marked lag phase is shown and also the fact that the time to reach an asymptote in is related to the phosphate concentration (e.g., 12 days at 0·5 μg P/l, 16 days at 2·5 μg 22 days at 25 μg P/l). The experiment was continued until an asymptote was reached level. The results can be arranged in another way, as in Fig. 33 where the initial concent phosphorus is plotted against the quantity of phosphorus used per cell. This is a linear re a log log plot. As the number of cells at the asymptote depends on the amount of growth taken place, the phosphorus used is clearly related to that quantity of growth. Fig 34 s same result in a different way. The relation between the growth and phosphorus uptake is cu and is represented as an arithmetic plot. Thus growth has been limited by limited phosph small number of divisions when all other elements are adequately present.

Since this work was completed, I have seen the paper by Goldberg, Walker and Wh (1951). Cultures of *Asterionella japonica* were grown and the phosphorus content of the was shown to be linearly dependent upon the phosphorus concentration in the medium. A

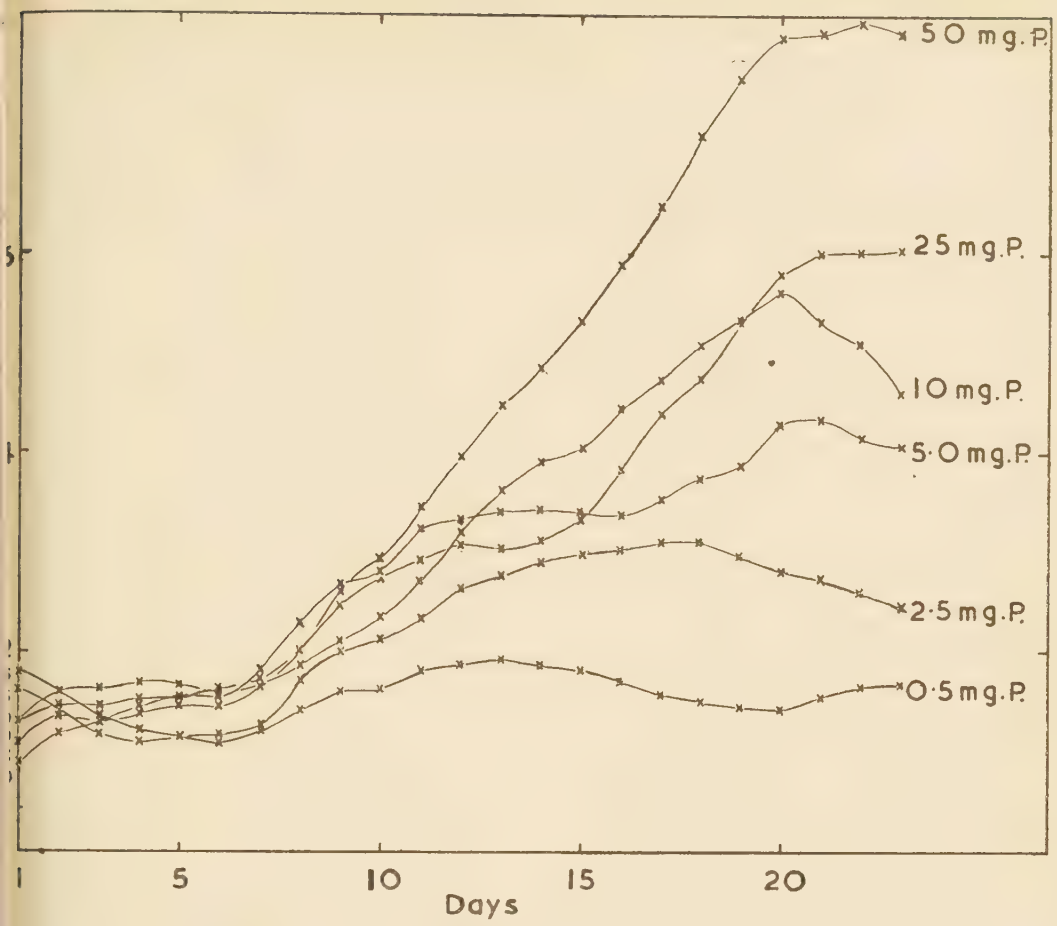


FIG. 32. THE RESULTS OF THE EXPERIMENT ON PHOSPHORUS UPTAKE AT THE SAME TEMPERATURE, BUT AT DIFFERENT PHOSPHORUS CONCENTRATIONS
The quantity of phosphorus is expressed as mg P/m.^{3} at the start of each experiment.

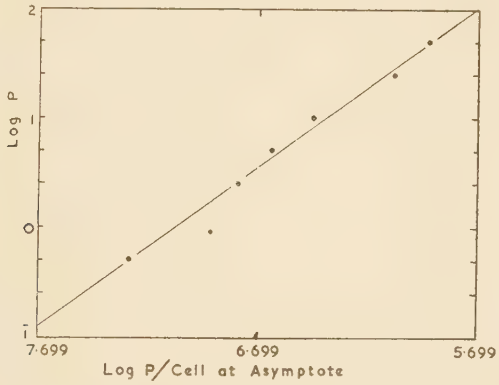


FIG. 33. THE INITIAL PHOSPHORUS CONCENTRATION PLOTTED AGAINST THE PHOSPHORUS CELL AT THE ASYMPTOTE
phosphorus/cell at the asymptote $\times 2 \times 10^{-6}$ is the phosphorus used in μg, divided by the number of cells produced by growth in numbers.

result is obtained from my data if the phosphorus used is divided amongst the initial number and not the asymptotic number. The linear relation of internal and external concentrations the question of whether the " phosphorus debt " of phosphorus-starved diatoms (Ketchum, s a debt, or whether the low level is due to low external phosphorus concentrations producing internal concentration.

However, there remains apparently the fact (Fig. 34) that a given amount of growth is rel the quantity of phosphorus taken up. If this applies over a longish period in the sea, then o attempt to extend the method of Harvey *et al.* (1935), of equating phosphorus depletion t volume, to the observations of phosphorus uptake made during the cruises. Measured variance of the mean of all phosphorus observations in the " A " group divided by the nur observations, the error is about 1 per cent. Consequently, the validity of values of phos depletion depends mainly upon the identification of water mass from cruise to cruise. It h

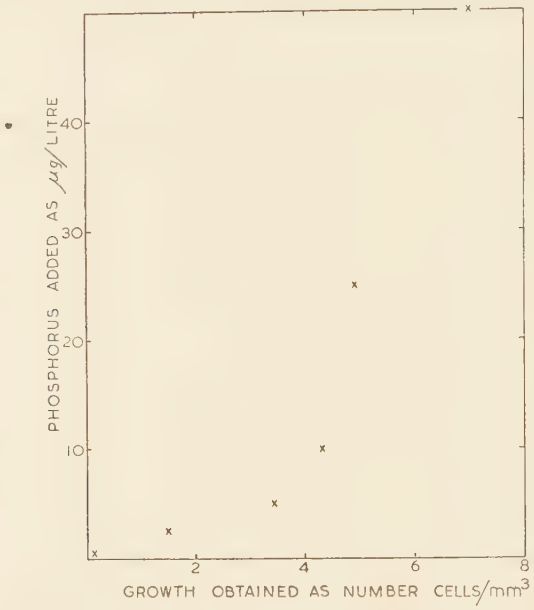


FIG. 34. THE RELATION BETWEEN PHOSPHORUS USED AND GROWTH IN NUMBERS

shown earlier that this is, for the " A " group of patches, valid for the first three cruises a will be used, although there is some increase in standard error owing to reduction of obse from 120 to 90. Phosphorus depletion will be converted into plant volume/litre, expresse this can be then related to the phosphorus content of sea water per litre. A stage in the co is the derivation of the factor by which the diatom concentrates the phosphorus in the sea a number of analyses (including those of Vinogradov, 1938), Sverdrup, Johnson and (1942) give a concentration factor of × 254,000.

The results of the two experiments described above may be used to derive concentration Factors from the first experiment are variable, whereas those from the second experim

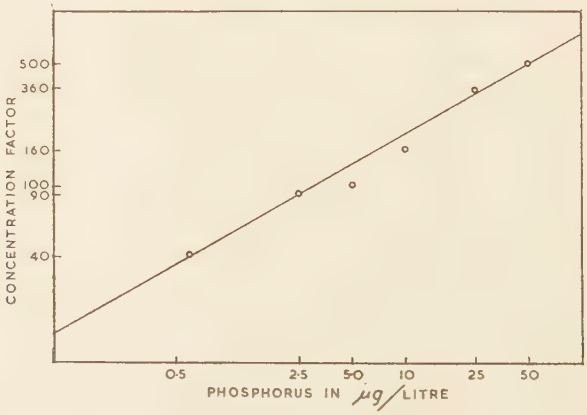


FIG. 35. THE RELATION BETWEEN PHOSPHORUS CONTENT OF THE MEDIUM AND THE CONCEN FACTOR × 10^{-3}

small error attached to them. This may well be due to the fact that the second experiment ırried out at a range of constant temperatures; it has been shown earlier that the rate of ıorus uptake varies with temperature. The way in which the concentration factors are l is shown in Table XXXVI.

concentration factor is used to make estimates of the quantities of phosphorus used from imates of plant production. The phosphorus content of 1 μ^3 of the sea in μg is multiplied concentration factor taken from Fig. 35 for the particular phosphorus content of the sea, the phosphorus content of 1 μ^3 of plant material.

Table XXXVI

Derivation of concentration factors (C). The quantity of phosphorus per μ^3 of medium (1 litre $\times$ 10^{-15}) is compared with the quantity of phosphorus per μ^3 of plant volume. *Phaeodactylum, Isochrysis galbana* and *Chlamydomonas* were the plants used.

Temperature and Phosphorus uptake experiments

Uptake μg–*at/l/cell/hr.*	*Div. rate per day*	*Time for 1 div. (hrs.)*	*Cell vol. in* μ^3	*Initial P* μg*/litre*	*Concentration factor*
Phaeodactylum					
$6{\cdot}27 \times 10^{-11}$	0·26	92	140	32	41,200
$2{\cdot}12 \times 10^{-10}$	0·26	91	140	44	100,200
$5{\cdot}47 \times 10^{-10}$	0·26	91	140	21	541,800
$2{\cdot}85 \times 10^{-10}$	0·31	76	140	27·4	180,700
$2{\cdot}12 \times 10^{-10}$	0·21	116	140	44	127,800
$6{\cdot}25 \times 10^{-11}$	0·23	106	140	32	47,300
Chlamydomonas					
$1{\cdot}26 \times 10^{-10}$	0·16	150	100	33	183,300
$5{\cdot}18 \times 10^{-11}$	0·19	123	100	27	75,500
$2{\cdot}14 \times 10^{-10}$	0·29	82	100	39	144,000
Isochrysis galbana					
$1{\cdot}23 \times 10^{-10}$	0·16	155	64	39	244,400
$4{\cdot}29 \times 10^{-11}$	0·30	80	64	63	27,200
$1{\cdot}12 \times 10^{-10}$	0·25	97	64	50	108,600
				Mean	151,833

Phosphorus concentration and Phosphorus uptake experiments

Phaeodactylum P. conc. μg*/litre*	*Increase in number cells* $\times 10^6$	*Cell volume in* μ^3	*Concentration factor*
0·5	86	140	41,500
2·5	198	140	90,200
5·0	344	140	103,800
10·0	432	140	165,300
25·0	493	140	362,200
50·0	704	140	507,300
110·0	520	140	1,511,000

In the temperature and phosphorus uptake experiments, the concentration factor is derive the following expression:

$$\frac{\text{Uptake } (\mu\text{g–at/cell/hr.}) \times \text{time for one division in hours} \times \text{atomic weight of phosphor}}{\text{Cell volume in } \mu^3 \times \text{initial phosphorus in } \mu\text{g}/\mu^3 \text{ of culture medium}}$$

In the phosphorus concentration and phosphorus uptake experiments, the concentration is derived from:

$$\frac{\text{Phosphorus concentration } (\mu\text{g}/\mu^3 \text{ of culture medium})}{\text{Growth obtained (number of cells)} \times \text{cell volume in } \mu^3 \times \text{atomic weight of phosphor}}$$

Table XXXVII

Comparison of estimates of phosphorus used (from production estimates) and the measured use

	Cruise VI	VII	VIII
(*a*) Phosphorus content	10·76	6·81	5·25 μg/litre
(*b*) Phosphorus loss ..	3·95	1·56	μg/litre
(*c*) Concentration factor ..	183,000	150,000	
(*d*) P/μ^3 of sea	8·785	6·03	$\mu g \times 10^{-15}$
(*e*) P/plant μ^3 ($c \times d$) ..	$1{\cdot}6077 \times 10^{-9}$	$9{\cdot}0450 \times 10^{-10}\mu g$	
(*f*) Counted plants ..	$4{\cdot}5675 \times 10^{24}$	$6{\cdot}6197 \times 10^{23}$	$2{\cdot}8188 \times 10^{22}$ μ^3
(*g*) Produced plants	$1{\cdot}2966 \times 10^{25}$	$1{\cdot}2844 \times 10^{24}$	μ^3
(*h*) Estimate of P used from production*	4·349	0·606	μg/litre
(*j*) Regeneration	0·399		μg/litre

*$\frac{\text{(Production in } \mu^3 \times \text{P/plant } \mu^3 \text{ in } \mu g)}{\text{(Volume of sea in litres (“A” patch))}}$

The quantity of phosphorus in one plant μ^3 is taken by finding the mean phosphorus of one μ^3 of sea water in the two cruises between which production was measured and by mu this by the appropriate concentration factor. Then the production between two cruises is m by the appropriate value of phosphorus in one plant μ^3 and the product is divided by the of sea in litres. This gives an estimated use of phosphorus derived from the estimate of pro The appropriate quantities and results are set out in Table XXXVII.

Between Cruises VI and VII the amount of phosphorus used from the production exceeds the measured loss by 0·4 μg/litre, or about 10 per cent. It is thought that this quan provided by regeneration. Thus $\frac{1}{10}$ of the phosphorus used in the dynamic cycle at this returned to the inorganic form within thirteen days. Regeneration must take place fro plant cells and from animal excreta; as the dynamic cycle can never theoretically stop, the also be some regeneration going on all the time. We see that, in order to estimate the regeneration and hence understand which are the most important factors contributing t must have an adequate measure of production. The present method used is not a complete of production, because some small and important diatoms were left out (*Nitzschia clo N. minutissimma* and *N. seriata*), many uncommon and unimportant diatoms were left o might, in sum, contribute a small part), two large diatoms were left out (*Rhizosolenia st* and *Coscinodiscus concinnus*), and lastly, all μ-flagellates and dinoflagellates were left out. is no reliable way of finding how complete an estimate of production has been made, using Steeman Nielsen's C^{14} method, which was not available in 1949. If the estimate of pro were 50 per cent of the true production, then 55 per cent of the phosphorus used would h regenerated to the inorganic form. If the estimate of production were 70 per cent of production, then 36 per cent of the phosphorus used would have been regenerated to the i form. It would be reasonable to suggest that the percentage regeneration lay between 10 and 30 per cent.

ween Cruises VII and VIII, however, the measured quantity of phosphorus used exceeds the timated from the production value by 0·954 μg/litre. The discrepancy here is the reverse of n the previous estimate and cannot be ascribed to regeneration. There are many possible odical reasons for this discrepancy, but a real one may be that the phosphorus samples in e VIII did not adequately cover the " A " patch.

concentration factor for larger diatoms may have a different character from that for smaller ns. So long as the predominant diatoms are all fairly small, a different characteristic for large ns would not make a very great difference to the calculations. By Cruise VIII, however, diatoms have become dominant in the normal planktonic succession and they may concentrate ter quantity of phosphorus as the surface/volume ratio is smaller for larger diatoms.

order to describe fully the dynamic cycle in the sea, proper account will have to be taken of eration, for as Harvey (1942) has rightly pointed out, the productivity of a region depends on mber of times that the phosphorus is put through the system. It is believed that the method bed above will, with proper observations, trace the course of regeneration during the early er. It is assumed that the only source of phosphorus in the sea is the soluble phosphate red by the molybdenum blue method. Chu (1946) has shown that phytin can be used by *onema costatum* and Rodhe (1948) has shown that *Scenedesmus quadricauda* can take up lic acid and convert it into growth. These can be considered as parts of the regenerative s. At the winter maximum, the organic phosphorus comprises about 10 per cent of the total trong and Harvey, 1950), which rises to 70 per cent at midsummer; the proportion of this n that is really available for growth is unknown. The quantity of soluble phosphorus ing to availability is thus a minimum measure of regeneration. Pratt's (1950) observations osphorus in fertilized sea water tanks showed that the rate of release of particulate phosphorus e water varied as the size of the plant standing crop. Regeneration of soluble phosphorus from rticulate form depends upon the rate of growth of the standing crop, which is to be expected if rticulate form is an intermediate stage in the regenerative process. This implies that the late form is less important to the plants than the soluble form. It follows from this that the f assimilation probably balances the rate of regeneration; this does not mean that they are but that as phosphorus is regenerated it becomes immediately available for assimilation. work was done in the absence of animals. Gardiner's (1937) results show that plankton ls excrete a form of phosphorus very rapidly, which is accessible to the molybdenum blue d. As this measures " soluble " phosphate, the presence of animals, breaking 90 per cent plant material down, is likely to accelerate the regenerative process.

6. Summary

basis of an analysis of productivity is an estimate of the standing crop of plants and of its f increase with time. It has been possible to estimate reproduction at the same time as the rs of diatoms. This has been made possible by the estimation of the diatom division rate neasurements of cell wall thickness made with an electron microscope.

duction was estimated for each of nine common diatom species. These were added to give volume in μ^3. This was apportioned according to the probable grazing capacities of each s stage, to give an estimate of the quantity of food taken by each copepodite stage of *Calanus*. near relation between the phosphorus content of *Phaeodactylum* and the phosphorus content medium has been shown. The concentration factors that may be read off this graph have sed to convert the estimates of production into estimates of phosphorus used. This, when sed, may lead to the measurement of regeneration.

Part VI

Production and the Feeding Fishery

We may make the generalization that pelagic fisheries depend on aggregations of fish aggregated fish may be conveniently caught. Whether the fisheries be near-water ones or ones, they may be divided into two types—spawning and feeding; in the first, the aggregatio shoals is an effect of spawning behaviour, and in the second it is an effect of the local prod of the sea. One may compare the East Anglian herring fishery, which is a fishery for ripen with the Shields fishery, which is a fishery for feeding fish; in the first, the shoals are very la in the second, they are quite small. Again, the feeding tunny are caught in the open o trolling for individuals that are feeding, but the spawning tunny may be caught in large i in beach " traps " in the Mediterranean, trapped by their behaviour.

A second generalization may be made: that because pelagic fisheries can stand a much catch than the demersal ones, the fish being more numerous, the depletion of stocks due t mortality is much less. Variations in the annual brood strength, called fluctuations, are conse of greater significance in pelagic fisheries. It has long been known that these variations ar to variations in production or in the winter maximum of phosphorus content (Russell, 1 has not been realized, however, that variations in production from place to place, of p patch to plankton patch in the summer, could give rise to differences in the availability o fish for catching.

The study of marine production started with Brandt (1899–1902). He applied the nitr phosporus cycles, worked out from soil chemistry, to the sea. This implied that the full of production was limited by the nitrogen or the phosphorus content. His second contribu to assess equivalent values for the different components of the production cycle. He estim diatoms, copepods and dinoflagellates, their content of protein, fat, carbohydrate, silicon, ash; from these values he estimated that 2,880 diatoms ≡ 85 to 101 dinoflagellates ≡ 0·78 copepods. Brandt's two ideas are the basis of all subsequent studies on the limitin of nutrients, and on the energy losses between trophic levels.

For a number of years, Atkins (1923 onwards) measured the variations within the year of phosphorus, silicon and radiation; he showed that the depletion of nitrogen and phosph related to the plant production. This work has been continued by Harvey in his wor effects of phosphorus, manganese, iron and growth factors on the growth of diatoms. Th is on the base of the system, the phosphorus content of the sea in the winter. This is a me potential productivity, i.e., the productivity that will take place in the subsequent season chemical index has the great advantage that it is easily measured and can be easily stand It can be used to compare the potential productivity of water masses in different regions.

Measures of actual production are made by estimating the standing crop of plants or he and at the same time its rate of increase; these measurements are made over a longish p an integration of the production of plants or herbivores over this period can be made.

There are two new features in the measurement of production in this paper. The first is plants themselves have been used, their numbers, volumes and division rates. Flemin wrote that he was " dealing with diatoms not as individuals . . . but with the ability of t population to fix carbon, nitrogen and phosphorus ". Fleming's concept means that th increase of the standing crop is estimated from a few observations on photosynthesis. B rate of photosynthesis can be used for this purpose, the effects of respiration and vertical tu must be separately estimated and incorporated into a " production increase coefficient new feature in this paper is that the three factors, photosynthesis, respiration and turbul not estimated separately, but that their net effect acting together is estimated as division r

Each system (plant, herbivore or fish) may be represented by an equation analogous to t in Section V for plant dynamics (Cushing, 1953). For example, the *Calanus* population

ed in terms of its reproduction rate and its death rate; its reproduction rate is dependent he production of plants and its death-rate is partly dependent upon the degree of aggregation ing. It is possible in this way to trace relationships all the way from the phosphorus content sea to the searching distributions of the drifters. These have not been set out fully in this because the method depends upon the proper sampling of one water mass between April ne; the identity of patch groups between cruises was only elucidated after the cruises had ompleted. As only three groups of patches were identified consecutively, there are only three ations of the *Calanus* distributions, only one of which is found to be associated with a able aggregation of pelagic fish. With further observations, the whole system could be ted in this way.

ier methods of dealing with the whole of the production cycle were concerned in essence with rcentage transfer of energy between trophic levels. These have been discussed in America man, 1942; Clarke, 1946) and in Russia (Ivlev, 1945). The dependence between levels is ed by Ivlev in the ecotrophic coefficient, which is the ratio of the sum of daily rations to the s of the food and its daily rate of increase. It is hoped that the methods developed in the paper will seem to represent some improvement.

gregation depends upon the recruitment into the larger stages of *Calanus*, and if this recruit- lepends upon the quantity of food available to each animal, and if this quantity depends he amount of radiation, the number of animals and on the nutrient limits, we have a fairly mechanism that may be studied. In practice, it will not be so simple, because in particular here will be dislocations of one process or another and variations in degree of different es; but it seems quite reasonable to expect the normal course of events to be predictable. actical point of studying the *Calanus* herring relation was to find the conditions that bring into catching concentrations at Shields.

e further practical points emerge from a study of production, arranged in this way. The nportant of these is fish movements. Firstly, there are the detailed movements of shoals an area of the size covered by the cruise grids. These movements are recorded directly by rvey, they are accounted for in terms of the production of *Calanus*. These could be exploited ers acting as a fleet, but it would need continuous survey to obtain the maximum profit from hod. Secondly, there are the variations in the shoal density and distribution that affect the ng behaviour of the fleet; again these may be measured empirically with an echo sounder; lerstanding will come only from a study of herring aggregation and disengagement. Again, obable that the exploitation of such herring shoals by a drifter fleet could often be improved anned method of searching, particularly if this were related to echo survey. A third point his study of production has thrown some light on to the movement of the herring on a larger It seems that they appear from the north edge of the Dogger and move into the deep water e contact with the food. Thus according to the duration of an aggregation system, so ably will the fish remain in the same water mass. This means that in years of poor production will stay where they are, but in years of rich production, they may move through greater es. So far, this is a reasonable extension of the facts that have been put forward in Part IV. er extension of this idea is that it provides a mechanism for profoundly mixing the herring rom year to year according to the production achieved. Herring stocks do become mixed tain extent and it is possible that this is the means by which this is brought about.

e points are by-products of the work. The study of production itself may be useful in two The mean weight of herring varies quite widely from year to year and it is probable that this o variations in food intake (Hodgson, 1950). The two variables can be related empirically, able prediction of mean weight can emerge only when the relation is understood. The way in which a study of production is useful is in the investigation of the availability of catching. This is the use of the *Calanus*-herring relation, for the availability off Shields upon the positions and duration of the local centres of production.

SUMMARY

As shown in the Introduction, analysis of the dynamic cycle requires four types of e:

(A) successive estimates of numbers of plankton populations in the same water mass; (B taneous estimates of the numbers of pelagic fish; (C) quantities of plant food taken each herbivores; (D) measures of the degree of phosphorus regeneration.

(A) In the estimation of plankton numbers, the following innovations were used:

1. A Petroff-Hausser counter was used with a Cole concentrator for the estima μ-flagellates.

2. Phytoplankton was estimated by the sedimentation method, using samples from a of depths and then mixing them into one.

3. An estimate of the use of a flowmeter is given. This is particularly valuable wh vertical hauls in bad weather. It also appears that the error of sampling is reduced in bad Plankton patches were contoured for numbers and identified from cruise to cruise by the described in Cushing (1953). From this technique rough age histograms were constru *Calanus finmarchicus*, which showed three points:

(i) *the heaviest mortality took place on copepodite stages IV, V and VI—about* 50 *fortnightly.*

(ii) *as the availability of plant food became reduced, recruitment to the naupliar st copepodite stage I was reduced,*

(iii) *the numbers of adults were small until the pelagic fish disengaged from the " C patch, and then they were quadrupled.*

(B) Indices of the numbers of pelagic fish were made by echo survey, as described in (1952). It was shown that pelagic fish aggregate on to the *Calanus* patches and then, aft disengage from them. The numbers in aggregation during three cruises (VII–IX) were five times; by Cruise X, numbers were reduced by half.

The degree of aggregation was measured by means of correlation coefficients. Aggreg greatest on *Calanus* copepodites stages IV and V, which also suffered the greatest mortalit

During the season studied, a transfer of aggregation from *Calanus* copepodites stage V t took place; it was shown that this was not due to differences in numbers or in biomass.

By analogy, a study of the aggregation of drifters on to herring patches was made in make use of the greater number of observations available. In November 1951, off Eas the greater the number of boats per square, the greater became the mean catch. At S May 1949, the situation was the reverse, because the greater the number of boats, the sn mean catch. This decrease could have been due to exploitation, net interference or en Examination of the coefficients of variation of these catches showed no relation between th of boats per square and coefficient of variation in November 1951, off East Anglia; of however, the coefficient increased with increasing number of boats and also decreasi catches per square. It was concluded that this must have been an effect of exploitation the fish could not have emigrated and net interference is ruled out because ships are mu together off East Anglia in November than they are off Shields in May.

Thus, a corollary of exploitation is the increased coefficient of variation. This is reas the shoals are being split up. By analogy, it is suggested that the transfer of aggregat *Calanus* copepodite stage V to stage IV is associated with the distribution of the stages appeared to be suffering a greater mortality.

It was pointed out that the cycle of aggregation on to and disengagement from a *Cala* that drifts with the southbound residual current provides a mechanism for mixing sh possibly stocks of pelagic fish.

From the decrease in cell size of the diatoms, estimates of division rate were obtained. These as follows:

Species	*Division rate per day*	
	Cruise VI-VII	*Cruise VII-VIII*
Rhizosolenia hebetata	0·355	0·226
Ditylum Brightwellii	0·415	0·681
Asterionella japonica	2·910	2·481
Chaetoceras compressus	1·145	0·456
Chaetoceras " densus "	0·858	0·665
Thalassiosira " gravida "	0·422	0·084
Lauderia borealis	0·097	0·139
Sceletonema costatum	0·569	0·353

ese figures have led to estimates of production, natural mortality and grazed plants between cruises:

	Cruise VI–VII	*Cruise VII–VIII*
Production	$12{,}966 \times 10^{21}\ \mu^3$	$1{,}284 \times 10^{21}\ \mu^3$
Total natural mortality ..	$187{\cdot}95 \times 10^{21}\ \mu^3$	$11{\cdot}96 \times 10^{21}\ \mu^3$
Total quantity grazed ..	$16{,}705 \times 10^{21}\ \mu^3$	$1{,}815 \times 10^{21}\ \mu^3$

e standing crop for Cruise VI was 0·192 gC/m.^{3}, with a daily production of 0·073 gC/m.^{3}; roduction coefficient is thus 38 per cent of the standing crop per day. Between Cruises VII VIII, the corresponding figures were:

Standing crop (Cruise VII)..	0·063 gc/m.^{3}
Production (Cruise VII–VIII)	0·014 gC/m.^{3}/day
Production coefficient	22 per cent/day

n these figures it is possible to estimate the quantity of food taken by each *Calanus* per day. een Cruises VI–VII, each *Calanus* stage V took 3·39 mm.^{3} of plant material per day; between ses VII–VIII, *Calanus* stage V took 0·179 mm.^{3} of plant material per day.

From experiments on phosphorus uptake by one species of small diatom, a concentration r for this diatom was derived. This factor was applied to all species of diatoms, perhaps stifiably. It was used to estimate the quantity of phosphorus used from the amount of uction. It was hoped that the difference between the estimate of phosphorus used, derived is way and the actual use of phosphorus, would give a measure of regeneration. This failed ve a quantitative result, because the value of production was a minimal one; the values, however, now the use of the method, which may give a quantitative result when the factors and coefficients been determined, in combination with the C^{14} method of estimating production, from a wider e of data.

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m grateful to my colleague, Mr. J. A. Gulland for helping me with the mathematics in Section 4, V (p. 62).

APPENDIX

Table I. Number of phytoplankton per litre. Cruises VI-IX, Sir Lancelot, 1949

CRUISE VI

Species \ *Station*	8	9	10	11	12	13	14	15	16	
DIATOMS:										
Asterionella japonica						1,100				
„ Dead										
Biddulphia mobiliensis		100							200	
„ regia		400								
„ sinensis										
Cerataulina bergoni				1,000	1,600					
Chaetoceras species		500								
„ brevis				600		4,100	1,800			
„ „ Dead						100				
„ compressus						1,700				
„ „ Dead										
„ decipiens										
„ densus	100				900	300				
„ „ Dead										
„ diadema										
„ „ Dead										
„ willei										
„ „ Dead										
Coscinodiscus radiatus									100	
Ditylum Brightwellii										
„ „ Dead										
Eucampia zoodiacus										
Gyrosigma		100								
Guinardia flaccida										
Hyalodiscus stelliger										
Lauderia borealis		300			4,800	1,200	5,500			
„ „ Dead										
Leptocylindrus danicus						500				
Navicula						400	200			
„ Dead										
Nitzschia closterium						100	200	300		
„ „ Dead								100		
„ delicatissima				400	600	1,000		2,300		
„ seriata										
Paralia sulcata	600	600				2,500	1,000			
Rhizosolenia alata										
„ hebetata	200	100		300	200	200				
„ shrubsolei										
„ Stolterfothii	1,300		1,800				1,400			
„ styliformis		500								
„ „ Dead		200								
Sceletonema costatum		300							500	2
„ „ Dead										
Surirella		100					100			
Thalassiosira gravida		2,400		1,400	700	5,300	2,700	700	300	1
„ „ Dead							300			
Thalassionema nitzschioides				500	500	3,400	200			
„ „ Dead										
TOTAL DIATOMS	2,200	5,600	1,800	4,200	9,300	21,900	13,400	3,400	1,100	4
DINOFLAGELLATES:										
Ceratium furca										
„ tripos										
Dinophysis rotundata										
TOTAL DINOFLAGELLATES										
SILICOFLAGELLATES:										
Distephanus speculum										
ZOOPLANKTON:										
Nauplii										

Station	19	20	21	22	23	24	25	26	27	28
japonica	1,000		7,200		3,200	24,700			12,300	2,000
„ .. .. Dead										
nobiliensis										
egia										
inensis										
bergoni			2,100		4,800	4,000			5,000	
species			2,600					200		
brevis	12,500	8,900	5,800			2,500			11,100	8,300
„ .. Dead	300									
compressus ..	1,800		1,600		11,000	19,500			16,900	3,800
„ .. Dead										
decipiens	600	200	400						700	
densus		400		200	1,200	800	500	1,000		
„ .. Dead										
diadema ..	700			300	700	1,000				
„ .. Dead										
willei										
„ .. Dead										
is radiatus										
ghtwellii		100			100				900	700
„ .. .. Dead									200	100
odiacus		600								
.. ..	100									
accida					200					
stelliger										
realis	1,700	13,200	21,000	7,100	4,300	1,400				
„ .. .. Dead		300	1,000	200	1,600	600				
us danicus			600							
.. ..	300					100	100		100	
.. .. .. Dead								100		
sterium	1,300	300				300	100	600	800	700
„ .. .. Dead			100					400	100	
licatissima	3,000	1,700	800	300	900	4,500			2,300	10,100
riata		500								1,400
ta							700			
alata								100		
hebetata		300	200	200	900	300		200		
shrubsolei										
Stolterfothii				800		500				
styliformis	100	700						100		
„ .. Dead										
costatum	3,600	1,000			700	2,300			3,400	27,800
„ .. Dead										200
.. ..	300	100					100			
gravida	62,600	131,100	99,400	60,600	44,500	59,700		400	700	28,600
„ .. Dead	1,500		600	300	600	300		100	900	11,400
ia nitzschioides ..	900	1,100	2,600		1,000				2,000	400
„ .. Dead										
OMS	92,300	160,500	146,000	70,000	75,700	122,500	1,500	3,200	57,400	95,500
TES:										
ca		100								
ipos										
otundata					100					
FLAGELLATES ..		100			100					
TES:										
speculum								200		
.. ..										

Species \ *Station*	29	31	32	33	34	35	36	37
DIATOMS:								
Asterionella japonica	14,200	54,600	6,300	23,400	19,800	38,300	52,700	93,200
„ „ Dead					300			
Biddulphia mobiliensis								
„ regia								
„ sinensis								
Cerataulina bergoni			300					
Chaetoceras species		3,000					9,400	1,600
„ brevis	12,900		3,900	900	6,400	12,000		8,000
„ „ Dead								
„ compressus	3,600	6,600	3,300		26,500	53,700	3,000	55,400
„ „ Dead								
„ decipiens							400	
„ densus					200			
„ „ Dead								
„ diadema		5,200						
„ „ Dead								1,200
„ willei								
„ „ Dead								
Coscinodiscus radiatus								
Ditylum Brightwellii	800	1,000	200		100	100	100	400
„ „ „ Dead								
Eucampia zoodiacus								
Gyrosigma								
Guinardia flaccida								
Hyalodiscus stelliger								
Lauderia borealis	1,100	6,400	3,400				1,300	
„ „ „ Dead			200					
Leptocylindrus danicus						2,200	800	
Navicula		200		200		100	200	
„ Dead								
Nitzschia closterium	1,100	1,600	200	500	700	200	700	800
„ „ „ Dead				100	100			
„ delicatissima	8,100	8,200	3,200	1,400	700	4,500	6,900	5,600
„ seriata		200				300		
Paralia sulcata				1,500				
Rhizosolenia alata								
„ hebetata			300					
„ shrubsolei								
„ Stolterfothii		600	1,100				1,900	
„ styliformis								
„ „ Dead								
Sceletonema costatum	7,900	5,600		7,100	5,100	3,100	2,300	5,200
„ „ Dead								
Surirella						100		
Thalassiosira gravida	69,800	87,400	66,100	1,400		500	12,400	12,000
„ „ Dead	15,700	5,000	5,600	1,300		200	400	1,200
Thalassionema nitzschioides	2,000	3,800	1,600	3,000	1,000	800		1,000
„ „ Dead			200		600		900	
TOTAL DIATOMS	137,200	189,400	95,900	40,800	61,500	116,100	93,400	185,600
DINOFLAGELLATES:								
Ceratium furca	100							
„ tripos								
Dinophysis rotundata								
TOTAL DINOFLAGELLATES	100							
SILICOFLAGELLATES:								
Distephanus speculum		400			100		100	
ZOOPLANKTON:								
Nauplii						100		

Station	40	41	42	43	44	45	46	47	48	49
ponica	52,400	26,700	4,100		4,800		700	29,300	600	4,700
„ .. Dead										
bbiliensis						200			100	600
;ia										
ensis					200				100	100
rgoni		1,200	1,100			800	100			
ecies	5,400		2,200	2,200			400			
brevis	9,500	8,800	10,500		2,200	300	7,800	2,000	2,000	
„ .. Dead	100		200							
compressus ..	30,700	41,200	13,200	2,900	1,000	600	900	14,000		1,800
„ .. Dead			600		300			500		
decipiens	1,000	1,200								300
densus					700	1,100	2,200	1,700	2,200	2,900
„ .. Dead							300			
diadema		200		2,100				1,300		
„ .. Dead				300						
willei					1,100					
„ .. Dead										
radiatus										
twellii	900	2,000	600							
, ... Dead	200	200								
diacus	800									100
.. ..										
cida										
elliger										
alis				9,000	1,400	2,500	1,200	6,500		1,200
„ .. .. Dead				1,700		300	300			
s danicus	600									
.. ..		200		100						
.. Dead										
terium	900	700	1,900	300		100	100	500	200	
„ .. Dead	200	100								
catissima	5,100	9,900	3,600	5,300	300	100	100	4,500	200	100
ata		600		1,600						
t		600	300	1,600						
alata										
hebetata				600	200	600	1,100	700		200
shrubsolei	100									
Stolterfothii				1,500			3,000	2,000		
styliformis					300					100
„ .. Dead										
ostatum	12,300	5,000	74,100	3,800						
„ .. Dead			2,000							
.. ..		100	100							
gravida	4,200	6,500	5,200	93,500	30,200	5,700	10,200	61,600		
„ .. Dead	300	2,100		3,000	300	500	1,000	300		
a nitzschioides ..		1,200	1,600	400	900		1,200		900	
„ .. Dead			400							
MS	124,700	108,500	121,700	129,900	43,900	12,800	30,600	124,900	6,300	12,100
ES:										
a						200				
pos							100			
tundata										
FLAGELLATES ..						200	100			
TES:										
peculum								100		
.. ..								100		100

Table I (*Contd.*)

CRUISE VII

Species \ Station	1	2	3	4	5	6	7	9	10
DIATOMS:									
Asterionella japonica ..	27,500	1,900			1,200	65,100	34,500	57,800	24,000
Bacillaria paradoxa ..				3,500					
Biddulphia mobiliensis ..									
Cerataulina bergoni ..	1,300	1,000				1,200	2,400	500	
Chaetoceras brevis ..	13,700	3,800				11,000	10,200	1,600	1,900
,, compressus ..	40,500	12,400	900	1,000		60,000	61,800	73,400	13,600
,, decipiens ..		600							
,, densus ..	400								
,, diadema ..		200		200					
Ditylum Brightwellii ..	400	1,800					400	300	
Eucampia zoodiacus ..							1,300		
Fragilaria species									
Lauderia borealis ..									
Leptocylindrus danicus ..							3,600		
Navicula species	200								
Nitzschia closterium ..	700	1,100	100		100	1,000	300	100	
,, delicatissima ..	5,200	1,000				300	6,200	1,000	
,, seriata									
Rhizosolenia delicatula ..									
,, hebetata ..									
,, shrubsolei ..				100					
,, Stolterfothii							400		
,, styliformis ..									
Sceletonema costatum ..	4,800	3,100					5,800	2,000	
Surirella									
Thalassiosira gravida ..	200	600					1,900		
Thalassionema nitzschioides		1,100							
TOTAL DIATOMS ..	94,900	28,600	1,000	4,800	1,300	138,600	128,800	136,700	39,500
DINOFLAGELLATES:									
Ceratium furca									
,, fusus						100			
,, macroceros ..									
Dinophysis norvegica ..									
Peridinium ovatum ..									
,, roseum ..									100
TOTAL DINOFLAGELLATES						100			100
Ptychocylis urnula									
Nauplius									

Station	14	15	17	18	19	20	21	23	24	25	26
a japonica ..	38,400	52,300	65,500								
aradoxa ..											
mobiliensis ..				100							
bergoni ..	2,600	1,800	2,700		500	600			900	2,000	
s brevis ..	20,400	8,600	14,900	1,000		4,000					
compressus ..	98,700	22,800	86,600								
decipiens ..		800									
densus ..										1,200	1,800
diadema ..											
ightwellii ..	1,300	500	200		100						
oodiacus ..	1,500										
pecies									100		
realis			800	1,100	5,500						
lrus danicus ..											
ecies						100					300
losterium ..	200	400	900	300	400	100			200	100	400
elicatissima ..	5,100	8,700	6,500	400	200	300			100		100
eriata			500	400	400						
a delicatula ..											200
hebetata ..				100	700		300				1,400
shrubsolei ..											
Stolterfothii											
styliformis ..											
a costatum ..	6,000	1,000	6,900	1,100							
.. .. ..									100		
a gravida ..			1,500	3,100	2,700	400					
ma nitzschioides	400										
OMS	174,600	96,900	187,000	7,600	10,500	5,500	300		1,400	3,300	4,200
LATES:											
rca						100					
sus											100
nacroceros											
norvegica ..									100		
ovatum ..											
oseum											
FLAGELLATES						100			100		100
nula				100							
.. .. ..				100							

Species \ Station	27	28	29	32	33	34	(S1)	35 (S2)	(S6)
DIATOMS:									
Asterionella japonica ..							6,700		
Bacillaria paradoxa ..									
Biddulphia mobiliensis ..									
Cerataulina bergoni ..	800		800		400				
Chaetoceras brevis ..							6,000	800	
,, compressus ..							11,700		
,, decipiens ..									
,, densus ..	400	200	100		400				
,, diadema ..							100	100	
Ditylum Brightwellii ..									
Eucampia zoodiacus ..									
Fragilaria species					200				
Lauderia borealis							1,000		
Leptocylindrus danicus ..							400	400	
Navicula species		100				100	1,600	600	100
Nitzschia closterium ..	800	200	300	1,100	500	1,000	3,900	7,900	
,, delicatissima ..									
,, seriata									
Rhizosolenia delicatula ..	1,000	1,300	700	600					100
,, hebetata ..									
,, shrubsolei ..	800	300	1,000		1,500				
,, Stolterfothii		100			100				
,, styliformis ..							9,800	34,000	
Sceletonema costatum ..		100					100		
Surirella	200					800	1,800	1,200	
Thalassiosira gravida ..									
Thalassionema nitzschioides									
TOTAL DIATOMS ..	4,000	2,300	2,900	1,700	3,100	1,900	43,100	45,000	200
DINOFLAGELLATES:									
Ceratium furca		100	200						
,, fusus						100			
,, macroceros ..									
Dinophysis norvegica ..	100	100							
Peridinium ovatum ..									
,, roseum ..									
TOTAL DINOFLAGELLATES	100	200	200			100			
Ptychocylis urnula							100		
Nauplius									

Table I (*Contd.*)

CRUISE VIII

Station	1	2	3	4	5	6	7	8	9	10	11
ponica ..				1,500				10,800	8,500		
rgoni ..			2,900	1,100				1,200	1,100		200
pecies ..					400						
orealis ..				6,000		2,600		600	2,400	600	
revis ..						1,900		1,800			
compressus ..				21,700	700	10,600		300			
decipiens ..				600							
densus ..						800					
diadema ..				4,900							
teres ..											
radiatus ..	100							100	100		
twellii ..						1,000		1,700			
diacus ..			100	1,200		5,100					
alis ..								1,000	1,300		
s danicus ..					100				100		
ies								800	400		100
terium ..		2,300	200		100		100	2,900		500	100
atissima ..				3,300		1,100					
ta		100	3,800			300					
nebetata ..			200								
shrubsolei ..			9,700			6,500		3,400	600		
Stolterfothii							800	3,000	200		
ostatum ..								100			
.. ..											
gravida ..			100		200						
a nitzschioides								500			
MS	100	2,400	17,000	40,300	1,500	29,900	900	28,200	14,700	1,100	400
ES:											
a						100					100
roceros ..			100								
s						100					
orvegica ..									100		
epressum ..							100				
atum ..											
FLAGELLATES			100			200	100		100		100
beroidea ..					100						
TES:											
speculum ..											
ius											100
.. ..									100		
.. ..	100					100			100		
.. ..											
ANKTON ..	100					100			200		100

Species \ *Station*	12	13	15	16	17	18	19	20	21
DIATOMS:									
Asterionella japonica ..									3,400
Cerataulina bergoni ..									4,200
Chaetoceras species ..									500
,, borealis ..									
,, brevis ..							300		3,600
,, compressus ..				100					
,, decipiens ..									
,, densus ..									
,, diadema ..									
,, teres ..									
Coscinodiscus radiatus ..	100								
Ditylum Brightwellii ..	100								
Eucampia zoodiacus ..									
Lauderia borealis ..	100								
Leptocylindrus danicus ..	700								500
Navicula species									
Nitzschia closterium ..		200	600				100		100
,, delicatissima ..	300	300	600	500			400		900
,, seriata									
Rhizosolenia hebetata ..	300			100					
,, shrubsolei ..									
,, Stolterfothii									3,100
Sceletonema costatum ..									
Surirella			100						
Thalassiosira gravida ..									
Thalassionema nitzschioides									
TOTAL DIATOMS ..	1,600	500	1,300	700			800		16,300
DINOFLAGELLATES:									
Ceratium furca	100	100		100					
,, macroceros ..	100			100				100	
,, tripos				100					
Dinophysis norvegica ..									100
Peridinium depressum ..									
,, ovatum ..								100	
TOTAL DINOFLAGELLATES	200	100		300				200	100
CILIATE:									
Tintinnopsis beroidea ..									
SILICOFLAGELLATES:									
Distephanus speculum ..				100					
ZOOPLANKTON									
Acartia nauplius									
Calanus ,, ...									
Nauplius									
Temora ,, ...									
TOTAL ZOOPLANKTON									

Station	24	25	26	27	28	29	30	31	32	33
ponica	1,300			300		900		1,000		
rgoni				3,500		200				
ecies										
borealis										
brevis							700			
compressus										
decipiens				500						
densus						200				
diadema										
eres										
radiatus										
twellii										
diacus										
alis										
s danicus						200			200	
es										
erium	100									100
tissima	200						500	1,100	400	
a										
ebetata										
hrubsolei										
tolterfothii										
ostatum			600			300	10,600	8,200	400	
.. ..				100		100				
gravida										
nitzschioides ..			1,000							
MS	1,600		1,600	4,400		1,900	11,800	10,300	1,000	100
s:										
t										
oceros										
.. .. ..										
rvegica					100					
ressum									100	
ttum										
LAGELLATES ..					100				100	
eroidea										
es:										
eculum										
is										
.. .. ..						100				
. .. .					100					
.. .. ..										
ANKTON					100	100				

Table I (*Contd.*)

CRUISE IX

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
DIATOMS:																													
Asterionella japonica ..						1,400																			2,400	200			
Cerataulina bergoni	400																												
Chaetoceras: species							800																						
borealis ..	500																												
densus	4,800																												
Coscinodiscus concinnus ..	400																								400				
Lauderia borealis																													
Navicula	100																								100			100	
Nitzschia: closterium ..																									22,100	5,300			
delicatissima ..		500					100																		400	1,200	2,200		
seriata																										100	100		
Rhizosolenia: hebetata ..																													
Stolterfothii ..	300																												
styliformis ..	300																												
Sceletonema costatum ..																									2,000	1,600			
Surirella									100										100									100	
Thalassiosira gravida																										600			
TOTAL DIATOMS	6,800	500				1,400	900		100										100						27,400	9,000	2,300	200	
DINOFLAGELLATES: Ceratium longipes										100																			
Prorocentrum micrans ..			100																										
TOTAL DINOFLAGELLATES			100							100																			
FLAGELLATES ..			900																									29,800	
PHAEOCYSTIS ..																													
ZOOPLANKTON:																											100		

Species	Calanus I		Calanus II		Calanus III		Calanus IV		Calanus V		Calanus ♂		Calanus ♀		Calanus Nauplius		Temora Longicornis		Paracal. Parvus ♂		Paracal. Parvus ♀		Paracal. Parvus Juv.		Pseudocal. El. ♂		Pseudocal. El. ♀		Pseudocal. El. Juv.	
(*Length mm*)^3	0·6787		1·8450		5·4351		12·4307		28·5292		44·3770		43·1185				2·406		1·416		0·982		0·825		1·920		5·071		2·048	
Station	*Depth (metres)*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*
1	41·5	—	—	—	—	—	—	—	—	—	—	—	—	0	0	—	—	2	83	—	—	—	—	2	83	—	—	2	83	3	124
2	53·0	—	—	1	53	—	—	1	53	0	0	—	—	2	106	—	—	—	—	—	—	1	53	—	—	1	53	1	53	4	212
3	51·2	6	307	2	102	1	51	1	51	0	0	—	—	1	51	1	51	3	154	—	—	4	205	3	154	2	102	9	461	17	870
4	47·0	6	282	4	188	7	329	4	188	3	141	0	0	3	141	—	—	18	846	—	—	24	1,128	12	564	12	564	36	1,692	78	3,666
5	32·9	3	99	3	99	8	263	8	263	2	66	—	—	—	—	—	—	34	1,119	—	—	—	—	—	—	8	263	8	263	28	921
6	18·0	—	—	7	126	4	72	3	54	1	18	—	—	—	—	4	72	56	1,008	—	—	—	—	—	—	4	72	13	234	19	342
7	34·7	8	278	8	278	2	69	2	69	0	0	—	—	—	—	—	—	40	1,388	—	—	8	278	—	—	—	—	—	—	8	278
8	32·9	28	921	28	921	8	263	5	164	1	33	—	—	0	0	—	—	208	6,843	—	—	—	—	—	—	—	—	—	—	97	3,191
9	34·7	29	1,006	29	1,006	68	2,360	6	208	2	69	—	—	0	0	—	—	214	7,426	—	—	10	347	—	—	—	—	19	659	58	2,013
10	23·8	15	357	30	714	42	1,000	5	119	1	24	0	0	0	0	—	—	333	7,925	—	—	—	—	—	—	—	—	15	357	—	—
11	29·3	58	1,699	44	1,289	29	850	5	146	2	59	0	0	0	0	29	850	175	5,128	—	—	—	—	—	—	—	—	44	1,289	15	440
12	31·1	—	—	41	1,275	95	2,954	14	435	7	218	0	0	0	0	14	435	352	10,947	—	—	14	435	—	—	54	1,679	—	—	81	2,519
13	51·0	23	1,173	6	306	17	867	11	561	5	255	0	0	1	51	—	—	69	3,519	—	—	34	1,734	—	—	6	306	23	1,173	63	3,213
14	71·0	6	426	13	923	6	426	7	497	6	426	1	71	1	71	19	1,349	109	7,739	—	—	19	1,349	6	426	45	3,195	97	6,887	103	7,313
15	65·0	7	455	7	455	7	455	43	2,795	1	65	0	0	1	65	58	3,770	7	455	—	—	—	—	7	455	—	—	7	455	79	5,135
16	57·0	8	456	8	456	25	1,425	3	171	1	57	0	0	10	570	8	456	—	—	—	—	16	912	—	—	8	456	16	912	16	912
17	57·0	24	1,368	16	912	8	456	3	171	3	171	0	0	3	171	16	912	—	—	—	—	8	456	8	456	8	456	8	456	16	912
18	60·0	38	2,280	8	480	23	1,380	6	360	2	120	—	—	1	60	176	10,560	77	4,620	—	—	15	900	8	480	15	900	38	2,280	107	6,420
19	64·0	33	2,112	50	3,200	42	2,688	8	512	4	256	0	0	2	128	133	8,512	58	3,712	—	—	—	—	—	—	8	512	25	1,600	92	5,888
20	80·0	6	480	6	480	6	480	6	480	2	160	0	0	0	0	46	3,680	51	4,080	—	—	17	1,360	—	—	6	480	29	2,320	46	3,680
21	69·0	22	1,518	38	2,622	27	1,863	13	897	3	207	0	0	0	0	43	2,967	92	6,348	—	—	—	—	—	—	—	—	5	345	76	5,244
22	37·0	34	1,258	57	2,109	23	851	21	777	5	185	0	0	1	37	126	4,662	183	6,771	—	—	—	—	—	—	—	—	—	—	103	3,811
23	70·0	30	2,100	17	1,190	13	910	12	840	5	350	0	0	0	0	9	630	178	12,460	—	—	4	280	4	280	4	280	13	910	22	1,540
24	70·0	38	2,660	15	1,050	30	2,100	18	1,260	7	490	—	—	—	—	76	5,320	182	12,740	—	—	—	—	—	—	—	—	15	1,050	38	2,660
25	76·8	90	6,912	75	5,760	98	7,526	18	1,382	4	307	1	77	2	154	15	1,152	117	8,986	4	307	4	307	19	1,459	8	614	26	1,997	15	1,152
26	75·0	79	5,925	65	4,875	26	1,950	17	1,275	6	450	0	0	3	225	26	1,950	124	9,300	—	—	7	525	33	2,475	7	525	13	975	59	4,425
27	75·0	13	975	26	1,950	26	1,950	33	2,475	12	900	3	225	1	75	20	1,500	7	525	—	—	—	—	—	—	—	—	7	525	59	4,425
28	82·3	27	2,222	7	576	20	1,646	9	741	3	247	0	0	1	82	60	4,938	7	576	—	—	—	—	—	—	7	576	20	1,646	47	3,868
29	59·0	28	1,652	43	2,537	43	2,537	23	1,357	18	1,062	2	118	6	354	114	6,726	128	7,552	—	—	14	826	—	—	—	—	14	826	142	8,378
30	62·0	60	3,720	53	3,286	40	2,480	11	682	4	248	1	62	2	124	73	4,526	33	2,046	—	—	20	1,240	13	806	—	—	7	434	73	4,526
31	77·0	31	2,387	31	2,387	39	3,003	19	1,463	4	308	1	77	2	154	16	1,232	31	2,387	—	—	—	—	—	—	—	—	31	2,387	39	3,003
32	64·0	31	1,984	47	3,008	23	1,472	14	896	3	192	0	0	1	64	47	3,008	94	6,016	—	—	8	512	—	—	—	—	8	512	23	1,472
33	82·0	18	1,476	23	1,886	23	1,886	6	492	10	820	1	82	6	492	6	492	35	2,870	—	—	12	984	12	984	6	492	18	1,476	29	2,378
34	76·8	—	—	4	307	9	691	3	230	5	384	3	230	4	307	13	998	4	307	—	—	—	—	9	691	—	—	4	307	47	3,610
35	82·3	15	1,234	15	1,234	7	576	7	576	7	576	2	165	3	247	44	3,621	22	1,811	—	—	4	329	11	905	—	—	18	1,481	22	1,811
36	82·3	13	1,070	27	2,222	40	3,292	24	1,975	10	823	1	82	4	329	13	1,070	31	2,551	—	—	4	329	4	329	9	741	13	1,070	27	2,222
37	69·5	36	2,502	48	3,336	66	4,587	54	3,753	16	1,112	2	139	4	278	6	417	30	2,085	—	—	6	417	—	—	6	417	18	1,251	36	2,502
38	73·0	—	—	—	—	5	365	5	365	3	219	1	73	1	73	—	—	11	803	—	—	—	—	—	—	—	—	—	—	38	2,774
39	69·0	5	345	—	—	22	1,518	17	1,173	6	414	2	138	3	207	—	—	16	1,104	—	—	—	—	—	—	—	—	11	759	22	1,518
40	64·0	42	2,688	21	1,344	35	2,240	34	2,176	6	384	1	64	1	64	14	896	42	2,688	—	—	—	—	—	—	—	—	—	—	7	448
41	69·0	6	414	24	1,656	11	759	7	483	2	138	0	0	0	0	12	828	18	1,242	—	—	—	—	6	414	6	414	—	—	30	2,070
42	62·2	18	1,120	—	—	2	124	7	435	1	62	0	0	0	0	—	—	18	1,120	—	—	—	—	—	—	9	560	18	1,120	36	2,239

Table II (*contd.*)

CRUISE VII

Species		Calanus I		Calanus II		Calanus III		Calanus IV		Calanus V		Calanus ♂		Calanus ♀		Calanus Nauplius		Temora Longicornis		Paracal. Parvus ♂		Paracal. Parvus ♀		Paracal. Parvus Juv.		Pseudocal. El. ♂		Pseudocal. El. ♀		Pseudocal. El. Juv.	
(*Length mm*)^3		0·6787		1·8450		5·4351		12·4307		28·5292		44·3770		43·1185				4·065		1·357		1·033		0·863		1·902		4·550		1·967	
Station	*Depth (metres)*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*
1	69·0	8	552	8	552	16	1,104	15	1,035	10	690	2	138	2	138	8	552	33	2,277	—	—	—	—	—	—	33	2,277	57	3,933	107	7,383
2	60·0	10	600	—	—	19	1,140	15	900	8	480	1	60	1	60	—	—	58	3,480	—	—	10	600	—	—	19	1,140	49	2,940	78	4,680
3	66·0	7	462	15	990	7	462	5	330	9	594	5	330	2	132	—	—	67	4,422	—	—	—	—	—	—	15	990	37	2 442	187	12,342
4	66·0	28	1,848	19	1,254	6	396	11	726	7	462	7	462	2	132	—	—	102	6,732	—	—	9	594	9	594	—	—	19	1,254	102	6,732
5	66·0	22	1,452	7	462	5	330	9	594	10	660	2	132	6	396	—	—	44	2,904	7	462	7	462	—	—	37	2,442	59	3,894	66	4,356
6	80·0	52	4,160	26	2,080	26	2,080	35	2,800	12	960	5	400	2	160	9	720	78	6,240	—	—	—	—	—	—	—	—	87	6,960	113	9,040
7																															
8	45·0	136	6,120	76	3,420	83	3,735	121	5,445	48	2,160	3	135	3	135	—	—	76	3,420	—	—	—	—	23	1,035	—	—	61	2,745	53	2,385
9	47·0	64	3,008	80	3,760	72	3,384	21	987	16	752	5	235	6	282	40	1,880	64	3,008	—	—	16	752	16	752	8	376	24	1,128	120	5,640
10	85·0	25	2,125	100	8,500	92	7,820	20	1,700	15	1,275	2	170	2	170	58	4,930	158	13,430	—	—	8	680	—	—	8	680	75	6,375	125	10,625
11	71·0	29	2,059	29	2,059	29	2,059	14	994	14	994	—	—	1	71	39	2,769	10	710	—	—	—	—	—	—	1	71	—	—	68	4,828
12	59·0	—	—	—	—	22	1,298	19	1,121	16	944	1	59	2	118	32	1,888	32	1,888	—	—	—	—	—	—	11	649	22	1,298	108	6,372
13	59·0	46	2,714	69	4,071	46	2,714	59	3,481	34	2,006	2	118	2	118	46	2,714	103	6,077	—	—	23	1,357	57	3,363	—	—	91	5,369	103	6,077
14	80·0	—	—	26	2,080	26	2,080	26	2,080	33	2,640	3	240	3	240	70	5,600	17	1,360	—	—	17	1,360	9	720	—	—	—	—	52	4,160
15	73·0	11	803	11	803	10	730	9	657	10	730	2	146	3	219	5	365	27	1,971	—	—	—	—	—	—	5	365	16	1,168	16	1,168
16	77·0	—	—	18	1,386	7	539	11	847	2	154	—	—	1	77	—	—	9	693	—	—	—	—	—	—	—	—	26	2,002	26	2,002
17	72·0	44	3,168	33	2,376	33	2,376	14	1,008	7	504	—	—	2	144	22	1,584	22	1,584	—	—	22	1,584	11	792	—	—	22	1,584	44	3,168
18	64·0	32	2,048	95	6,080	71	4,544	15	960	2	128	1	64	1	64	8	512	55	3,520	—	—	16	1,024	8	512	16	1,024	24	1,536	63	4,032
19	75·0	5	375	21	1,575	74	5,550	5	375	4	300	—	—	1	75	5	375	42	3,150	—	—	—	—	5	375	—	—	16	1,200	5	375
20	75·0	19	1,425	29	2,175	29	2,175	40	3,000	36	2,700	2	150	2	150	10	750	96	7,200	10	750	10	750	19	1,425	10	750	10	750	48	3,600
21	74·0	—	—	38	2,812	51	3,774	17	1,258	15	1,110	1	74	—	—	—	—	64	4,736	—	—	19	1,406	19	1,406	6	444	26	1,924	38	2,812
22	70·0	18	1,260	54	3,780	63	4,410	62	4,340	14	980	—	—	1	70	—	—	126	8,820	—	—	9	630	9	630	—	—	27	1 890	45	3,150
23	55·0	32	1,760	26	1,430	136	7,480	123	6,765	60	3,795	5	275	14	770	6	330	201	11,055	6	330	—	—	6	330	13	715	65	3,575	19	1,045
24	67·0	15	1,005	15	1,005	22	1,474	37	2,479	13	871	—	—	—	—	—	—	52	3,484	—	—	15	1,005	37	2,479	15	1,005	45	3,015	22	1,474
25	70·0	39	2,730	59	4,130	111	7,770	85	5,950	55	3,850	5	350	17	1,190	—	—	131	9,170	—	—	52	3,640	65	4,550	7	490	52	3,640	72	5,040
26	55·0	—	—	44	2,420	106	5,830	64	3,520	19	1,045	2	110	3	165	9	495	415	22,825	—	—	9	495	18	990	18	990	26	1,430	62	3,410
27	35·0	—	—	24	840	24	840	12	420	2	70	—	—	2	70	—	—	142	4,970	—	—	2	70	2	70	3	105	3	105	9	315
28	28·0	10	280	27	756	23	644	40	1,120	4	112	—	—	0	0	—	—	550	15,400	—	—	10	280	3	84	3	84	20	560	43	1,204
29	29·0	3	87	3	87	44	1,276	9	261	2	58	—	—	—	—	—	—	146	4,234	—	—	17	493	15	435	9	261	12	348	29	841
30																															
31																															
32	29·0	—	—	21	609	0	0	0	0	1	29	0	0	—	—	—	—	229	6,641	—	—	4	116	4	116	21	609	4	116	29	841
33																															
34	51·0	35	1.785	26	1.326	44	2.244	6	306	5	255	—	—	3	153	70	3.570	61	3.111	—	—	—	—	9	459	26	1.326	44	2.244	244	12 444

Species		Calanus I		Calanus II		Calanus III		Calanus IV		Calanus V		Calanus ♂		Calanus ♀		Calanus Nauplius		Temora Longicornis		Paracal. Parvus ♂		Paracal. Parvus ♀		Paracal. Parvus Juv.		Pseudocal. El. ♂		Pseudocal. El. ♀		Pseudocal. El. Juv.	
(Length mm)³		0·6787		1·8450		5·4351		12·4307		28·5292		44·3770		43·1185				4·252		1·191		1·012		0·744		1·631·		4·267		1·379	
Station	Depth (metres)	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre
1	35·0	—	—	5	175	29	1,015	24	840	7	245	0	0	0	0	—	—	1,063	37,205	—	—	24	840	24	840	24	840	48	1,680	169	5,915
2	31·1	—	—	3	93	18	560	18	560	7	218	—	—	0	0	—	—	731	22,734	—	—	—	—	—	—	29	902	29	902	146	4,541
3	29·3	—	—	8	234	4	117	23	674	7	205	—	—	—	—	—	—	198	5,801	—	—	—	—	—	—	—	—	119	3,487	159	4,659
4	53·0	54	2,862	7	371	36	1,908	14	742	4	212	0	0	1	53	54	2,862	143	7,579	—	—	90	4,770	72	3,816	72	3,816	125	6,625	341	18,073
5	67·0	—	—	0	0	0	0	4	268	3	201	0	0	1	67	15	1,005	58	3,886	—	—	44	2,948	58	3,886	58	3,886	88	5,896	307	20,569
6	73·0	52	3,796	116	8,468	52	3,796	54	3,942	28	2,044	5	365	3	219	90	6,570	284	20,732	—	—	65	4,745	52	3,796	78	5,694	103	7,519	465	33,945
7	60·0	9	540	47	2,820	85	5,100	92	5,520	13	780	1	60	1	60	19	1,140	57	3,420	—	—	38	2,280	57	3,420	28	1,680	9	540	170	10,200
8	51·2	12	614	25	1,280	99	5,069	30	1,536	15	768	5	256	7	358	25	1,280	74	3,789	—	—	49	2,509	62	3,174	25	1,280	49	2,509	148	7,578
9	56·7	56	3,175	28	1,588	69	3,912	11	624	10	567	—	—	3	170	28	1,588	181	10,263	—	—	56	3,175	83	4,706	42	2,381	97	5,500	278	15,763
10	62·2	31	1,928	31	1,928	46	2,861	102	6,344	31	1,928	3	187	—	—	—	—	154	9,579	—	—	—	—	31	1,928	46	2,861	15	933	386	24,009
11	67·7	71	4,807	59	3,994	106	7,176	90	6,093	38	2,573	—	—	—	—	130	8,801	343	23,221	—	—	177	11,983	213	14,420	130	8,801	154	10,426	934	63,232
12	82·3	21	1,728	28	2,304	13	1,070	49	4,033	18	1,481	—	—	1	82	14	1,152	302	24,855	—	—	42	3,457	63	5,185	7	576	35	2,880	394	32,426
13	69·5	—	—	3	208	5	348	5	348	16	1,112	—	—	1	70	—	—	323	22,448	—	—	—	—	26	1,807	13	904	26	1,807	52	3,614
14	64·0	20	1,280	10	640	60	3,840	28	1,792	12	768	2	128	2	128	—	—	615	39,360	—	—	40	2,560	40	2,560	40	2,560	50	3,200	139	8,896
15	65·8	12	790	6	395	24	1,579	11	724	5	329	0	0	0	0	6	395	519	34,150	6	395	6	395	31	2,040	6	395	37	2,435	147	9,673
16	73·0	8	584	8	584	64	4,672	37	2,701	29	2,117	3	219	—	—	—	—	365	26,645	—	—	24	1,752	16	1,168	8	584	24	1,752	87	6,351
17	66·0	8	528	60	3,960	83	5,478	57	3,762	53	3,498	2	132	14	924	23	1,518	496	32,736	—	—	60	3,960	83	5,478	23	1,518	98	6,468	511	33,726
18	78·0	—	—	8	624	71	5,538	127	9,906	46	3,588	6	468	3	234	16	1,248	349	27,222	—	—	48	3,744	64	4,992	16	1,248	95	7,410	873	68,094
19	80·0	—	—	—	—	2	160	18	1,440	9	720	—	—	—	—	—	—	111	8,880	11	880	—	—	11	880	—	—	—	—	133	10,640
20	62·2	47	2,923	47	2,923	47	2,923	57	3,545	66	4,105	7	435	7	435	47	2,923	260	16,172	—	—	83	5,163	47	2,923	24	1,493	83	5,163	520	32,344
21	78·6	23	1,808	31	2,437	22	1,729	30	2,358	20	1,572	1	79	2	157	31	2,437	157	12,340	—	—	16	1,258	8	629	39	3,065	16	1,258	243	19,100
22	82·3	8	658	—	—	7	576	20	1,646	20	1,646	1	82	—	—	25	2,058	139	11,440	—	—	16	1,317	8	658	57	469	155	12,756	188	15,472
23	49·4	—	—	40	1,976	66	3,260	26	1,284	24	1,186	8	395	5	247	—	—	79	3,903	—	—	53	2,618	26	1,284	53	2,618	397	19,612	1,058	52,265
24	53·0	—	—	26	1,378	35	1,855	53	2,809	21	1,113	2	106	11	583	18	954	212	11,236	—	—	26	1,378	18	954	18	954	115	6,095	265	14,045
25	73·0	—	—	13	949	47	3,431	39	2,847	24	1,752	1	73	5	365	—	—	40	2,920	—	—	—	—	—	—	—	—	7	511	134	9,782
26	70·0	7	490	21	1,470	63	4,410	47	3,290	11	770	—	—	1	70	—	—	111	7,770	—	—	—	—	—	—	7	490	14	980	63	4,410
27	80·0	20	1,600	30	2,400	40	3,200	28	2,240	6	480	0	0	0	0	—	—	91	7,280	—	—	—	—	10	800	—	—	20	1,600	20	1,600
28	78·6	8	629	—	—	34	2,672	45	3,537	10	786	1	79	2	157	17	1,336	202	15,877	—	—	25	1,965	25	1,965	—	—	93	7,310	194	15,248
29	78·6	30	2,358	48	3,773	14	1,100	54	4,244	35	2,751	—	—	6	472	6	472	167	13,126	—	—	30	2,358	36	2,830	6	472	30	2,358	269	21,143
30	69·5	—	—	33	2,294	98	6,811	56	3,892	52	3,614	—	—	13	904	16	1,112	311	21,614	—	—	33	2,294	33	2,294	33	2,294	131	9,104	474	32,943
31	69·5	—	—	12	834	37	2,572	17	1,182	19	1,320	1	70	2	139	—	—	94	6,533	—	—	25	1,738	56	3,892	31	2,154	119	8,270	537	37,322
32	64·0	—	—	36	2,304	17	1,088	19	1,216	7	448	1	64	1	64	14	896	100	6,400	—	—	7	448	14	896	50	3,200	128	8,192	577	36,928
33	40·0	—	—	16	640	79	3,160	13	520	22	880	11	440	11	440	—	—	175	7,000	—	—	16	640	48	1,920	48	1,920	254	10,160	429	17,160
34	42·1	3	126	—	—	5	210	5	210	4	168	1	42	2	84	—	—	26	1,095	—	—	3	126	3	126	26	1,095	26	1,095	155	6,526
35	53·0	30	1,590	30	1,590	10	530	55	2,915	97	5,141	44	2,332	26	1,378	10	530	20	1,060	—	—	10	530	—	—	20	1,060	71	3,763	162	8,586
36	36·0	54	1,944	12	432	3	108	10	360	3	108	0	0	0	0	30	1,080	48	1,728	—	—	30	1,080	36	1,296	30	1,080	72	2,592	242	8,712
37	32·9	64	2,106	79	2,599	4	132	22	724	8	263	1	33	3	99	127	4,178	222	7,304	16	526	127	4,178	175	5,758	111	3,652	381	12,535	667	21,944
38	42·1	—	—	—	—	0	0	1	42	1	42	0	0	0	0	12	505	12	505	—	—	12	505	86	3,621	25	1,052	74	3,115	370	15,577
39	12·8	—	—	—	—	0	0	9	115	5	64	—	—	0	0	—	—	267	3,418	—	—	111	1,421	178	2,278	222	2,842	778	9,958	1,378	17,638

Table II (*contd.*)

CRUISE IX

Species		Calanus I		Calanus II		Calanus III		Calanus IV		Calanus V		Calanus ♂		Calanus ♀		Calanus Nauplius		Temora Longicornis		Paracal. Parvus ♂		Paracal. Parvus ♀		Paracal. Parvus Juv.		Pseudocal. El. ♂		Pseudocal. El. ♀		Pseudocal. El. Juv.	
(*Length mm*)^3		0·6787		1·8450		5·4351		12·4307		28·5292		44·3770		43·1185				2·617		1·112		0·994		0·707		1·364		3·288		1·198	
Station	*Depth (metres)*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*	*No. per metre cubed*	*No. beneath one sq. metre*
1	51·2	—	—	22	1,126	6	307	6	307	8	410	1	51	2	102	11	563	86	4,403	22	1,126	65	3,328	65	3,328	119	6,093	421	21,555	1,553	79,514
2	75·0	21	1,575	10	750	21	1,575	35	2,625	49	3,675	2	150	10	750	31	2,325	174	13,050	—	—	21	1,575	82	6,150	21	1,575	328	24,600	1,323	99,225
3	64·0	15	960	15	960	46	2,944	150	9,600	73	4,672	3	192	—	—	—	—	580	37,120	—	—	61	3,904	92	5,888	46	2,944	92	5,888	961	61,504
4	60·3	13	784	—	—	28	1,688	36	2,171	56	3,377	—	—	13	784	—	—	192	11,578	—	—	—	—	64	3,859	13	784	13	784	153	9,226
5	47·5	16	760	30	1,425	56	2,660	79	3,752	40	1,900	16	760	—	—	—	—	873	41,468	—	—	—	—	33	1,568	49	2,328	214	10,165	313	14,868
6	54·9	—	—	2	110	7	384	10	549	19	1,043	5	274	14	769	—	—	420	23,058	—	—	17	933	26	1,427	9	494	26	1,427	240	13,176
7	66·0	8	528	16	1,056	23	1,518	28	1,848	28	1,848	3	198	2	132	—	—	149	9,834	—	—	8	528	31	2,046	—	—	23	1,518	47	3,102
8	68·0	—	—	—	—	36	2,448	89	6,052	80	5,440	7	476	7	476	—	—	276	18,768	7	476	29	1,972	36	2,448	15	1,020	87	5,916	335	22,780
9	86·0	—	—	—	—	46	3,956	15	1,290	10	860	1	86	1	86	—	—	441	37,926	—	—	—	—	7	602	13	1,118	33	2,838	86	7,396
10	71·0	—	—	13	1,118	13	923	39	2,769	39	2,769	1	71	2	142	—	—	251	17,821	—	—	45	3,195	22	1,562	—	—	11	781	78	5,538
11	51·2	—	—	7	497	15	768	23	1,178	47	2,406	3	154	3	154	—	—	1,210	61,952	8	410	42	2,150	42	2,150	17	870	25	1,280	317	16,230
12	65·8	—	—	—	—	12	790	66	4,343	46	3,027	3	197	1	66	—	—	699	45,994	7	461	66	4,343	22	1,448	—	—	44	2,895	353	23,227
13	84·1	—	—	3	197	12	1,009	72	6,055	39	3,280	5	420	6	505	—	—	495	41,630	—	—	54	4,541	66	5,551	—	—	30	2,523	328	27,585
14	65·8	—	—	—	—	2	132	21	1,382	35	2,303	2	132	6	395	—	—	452	29,742	—	—	10	658	10	658	10	658	87	5,725	144	9,475
15	58·6	—	—	2	132	2	132	21	1,382	35	2,303	2	132	6	395	—	—	467	27,366	8	469	24	1,406	32	1,875	8	469	55	3,223	261	15,295
16	82·3	16	938	8	469	6	352	40	2,344	43	2,520	2	117	2	117	—	—	252	20,740	—	—	31	2,551	69	5,679	31	2,551	84	6,913	145	11,934
17	62·2	—	—	9	741	12	988	61	5,020	79	6,502	9	741	12	988	—	—	597	37,133	—	—	—	—	9	560	9	560	228	14,182	275	17,105
18	71·0	19	1,182	28	1,742	38	2,364	82	5,100	55	3,421	2	124	17	1,057	—	—	287	20,377	—	—	9	639	9	639	9	639	26	1,846	165	11,715
19	80·0	2	142	5	355	10	710	54	3,834	28	1,988	5	355	5	355	—	—	232	18,560	—	—	—	—	9	720	—	—	89	7,120	116	9,280
20	80·0	9	720	36	2,880	36	2,880	36	2,880	25	2,000	—	—	2	160	—	—	594	47,520	—	—	—	—	31	2,480	31	2,480	63	5,040	282	22,560
21	68·0	10	800	31	2,480	29	2,320	33	2,640	46	3,680	—	—	6	480	—	—	404	27,472	—	—	20	1,360	40	2,720	—	—	40	2,720	336	22,848
22	68·0	7	476	7	476	47	3,196	59	4,012	38	2,584	—	—	3	204	—	—														
23	79·0	—	—	14	1,106	28	2,212	49	3,871	32	2,528	3	237	4	316	—	—	389	30,731	—	—	7	553	14	1,106	—	—	21	1,659	97	7,663
24	70·0	18	1,260	18	1,260	44	3,080	37	2,590	35	2,450	2	140	12	840	9	630	282	19,740	9	630	18	1,260	—	—	—	—	62	4,340	150	10,500
25	67·0	7	469	12	804	10	670	15	1,005	12	804	10	670	12	804	42	2,814	83	5,561	—	—	42	2,814	8	536	17	1,139	83	5,561	187	12,529
26	66·0	2	132	1	66	3	198	1	66	2	132	9	594	4	264	9	594	56	3,696	—	—	—	—	9	594	47	3,102	140	9,240	196	12,906
27	40·2	—	—	—	—	—	—	2	80	6	241	7	281	22	884	13	523	91	3,658	—	—	—	—	—	—	—	—	78	3,136	169	6,794
28	69·5	—	—	—	—	1	70	3	208	8	556	1	70	5	348	—	—	382	26,549	—	—	13	904	19	1,320	38	2,641	275	19,112	275	19,112
29	87·8	6	527	—	—	2	176	5	439	9	790	5	439	8	702	—	—	273	23,969	—	—	—	—	—	—	6	527	74	6,497	51	4,478

Species		Calanus I		Calanus II		Calanus III		Calanus IV		Calanus V		Calanus ♂		Calanus ♀		Calanus Nauplius		Temora Longicornis		Paracal. Parvus ♂		Paracal. Parvus ♀		Paracal. Parvus Juv.		Pseudocal. El. ♂		Pseudocal. El. ♀		Pseudocal. El. Juv.	
(Length mm)³		0·6787		1·8450		5·4351		12·4307		28·5292		44·3770		43·1185				1·794		0·935		0·839		0·649		1·239		2·428		1·086	
Station	Depth (metres)	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre	No. per metre cubed	No. beneath one sq. metre
1	18·3	—	—	—	—	—	—	1	18	1	18	1	18	0	0	—	—	686	12,554	—	—	34	622	34	622	34	622	34	622	686	12,554
2	25·6	—	—	—	—	3	77	10	256	2	51	—	—	0	0	—	—	29	742	29	742	146	3,738	321	8,218	58	1,485	146	3,738	437	11,187
3	32·9	—	—	5	164	18	592	20	658	6	197	1	33	1	33	—	—	188	6,185	—	—	—	—	—	—	—	—	—	—	—	—
4	53·0	—	—	4	212	16	848	32	1,696	13	689	—	—	—	—	—	—	30	1,590	—	—	121	6,413	80	4,240	20	1,060	161	8,533	432	22,896
5	43·9	—	—	—	—	2	88	9	395	43	1,888	18	790	23	1,010	46	2,019	114	5,005	—	—	23	1,010	46	2,019	11	483	160	7,024	2,000	87,800
6	49·4	—	—	—	—	—	—	4	198	9	445	9	445	5	247	—	—	405	20,007	—	—	10	494	30	1,482	—	—	247	12,202	593	29,294
7	54·9	10	549	—	—	1	55	11	604	3	165	—	—	0	0	30	1,647	179	9,827	—	—	30	1,647	40	2,196	10	549	20	1,098	1,096	60,170
8	36·6	18	659	88	3,221	42	1,537	113	4,136	11	403	—	—	—	—	—	—	247	9,040	18	659	71	2,599	53	1,940	71	2,599	230	8,418	1,431	52,375
9	42·1	—	—	18	758	7	295	29	1,221	29	1,221	—	—	—	—	—	—	91	3,831	18	758	164	6,904	55	2,316	55	2,316	91	3,831	565	23,786
10	14·6	42	613	—	—	2	29	16	234	6	88	1	15	1	15	208	3,037	—	—	—	—	208	3,037	—	—	42	613	208	3,037	583	8,512
11	18·3	—	—	8	146	4	73	25	458	24	439	3	55	5	92	—	—	39	714	—	—	155	2,836	78	1,427	194	3,550	155	2,836	699	12,792
12	27·4	18	493	27	740	18	493	9	247	49	1,343	9	247	4	110	—	—	1,121	30,715	—	—	135	3,699	90	2,466	45	1,233	852	23,345	2,825	77,405
13	43·9	—	—	3	132	3	132	10	439	22	966	3	132	3	132	13	571	482	21,160	25	1,098	152	6,673	165	7,244	152	6,673	405	17,780	2,180	95,702
14	69·5	—	—	—	—	6	417	56	3,892	63	4,378	14	973	4	278	—	—	811	56,364	6	417	25	1,738	51	3,544	13	904	139	9,660	963	66,928
15	60·3	—	—	—	—	4	241	78	4,703	54	3,256	6	362	9	543	—	—	842	50,773	—	—	19	1,146	19	1,146	—	—	56	3,377	722	43,537
16	60·3	—	—	5	302	23	1,387	56	3,377	47	2,834	14	844	16	965	—	—	—	—	—	—	27	1,628	45	2,714	18	1,085	126	7,598	753	45,406
17	60·3	31	1,809	2	121	8	482	20	1,206	25	1,508	12	724	25	1,508	—	—	665	40,100	—	—	20	1,206	41	2,472	10	603	72	4,342	460	27,738
18	54·9	—	—	—	—	3	165	6	329	9	494	15	824	10	549	10	549	850	46,665	—	—	10	549	10	549	10	549	40	2,196	405	22,234
19	69·5	—	—	—	—	1	70	18	1,251	9	626	4	278	4	278	—	—	474	32,943	—	—	7	486	—	—	29	2,016	51	3,544	408	28,356
20	76·8	40	3,072	40	3,072	12	922	113	8,678	157	12,058	8	614	28	2,150	—	—	8,342	640,666	20	1,536	121	9,293	221	16,973	40	3,072	201	15,437	1,608	123,494
21	65·8	—	—	—	—	16	1,053	30	1,974	31	2,040	9	592	17	1,119	—	—	1,848	121,598	7	461	28	1,842	43	2,829	14	921	43	2,829	562	36,980
22	67·7	—	—	—	—	—	—	8	542	9	609	2	135	8	542	—	—	1,441	97,556	—	—	16	1,083	5	338	22	1,489	110	7,447	242	16,383
23	65·8	—	—	—	—	—	—	17	1,119	55	3,619	12	790	27	1,777	—	—	1,377	90,607	—	—	25	1,645	50	3,290	12	790	17	1,119	819	53,890
24	69·5	—	—	—	—	5	348	63	4,378	97	6,742	22	1,529	17	1,182	—	—	1,345	93,478	—	—	9	626	—	—	9	626	26	1,807	315	21,892
25	64·0	—	—	—	—	8	512	22	1,408	9	576	8	512	189	12,096	—	—	378	24,192	—	—	32	2,048	32	2,048	—	—	32	2,048	544	34,816
26	65·8	—	—	9	592	9	592	36	2,369	29	1,908	4	263	8	526	—	—	764	50,271	—	—	13	855	13	855	7	461	27	1,777	248	16,318
27	65·8	—	—	—	—	10	658	33	2,171	36	2,369	7	461	23	1,513	—	—	1,100	72,380	8	526	16	1,053	16	1,053	—	—	90	5,922	583	38,361
28	82·3	—	—	30	2,469	4	329	7	576	16	1,317	7	576	13	1,070	7	576	487	40,080	7	576	7	576	7	576	22	1,811	103	8,477	627	51,602
29	82·3	31	2,551	77	6,337	46	3,786	9	741	15	1,234	3	247	12	988	8	658	514	42,302	—	—	15	1,234	23	1,893	15	1,234	107	8,806	851	70,037
30	60·3	2	121	—	—	0	0	0	0	2	121	1	60	1	60	—	—	442	26,653	—	—	—	—	18	1,085	53	3,196	177	10,673	601	36,240
31	64·0	41	2,624	108	6,912	41	2,624	34	2,176	30	1,920	—	—	3	192	—	—	285	18,240	—	—	34	2,176	20	1,280	14	896	102	6,528	291	18,624
32	71·4	137	9,782	216	15,422	147	10,496	16	1,142	10	714	2	143	5	357	10	714	206	14,708	—	—	—	—	—	—	20	1,428	49	3,499	265	18,921
33	54·9	194	10,651	450	24,705	501	27,505	131	7,192	14	769	—	—	2	110	—	—	143	7,851	—	—	—	—	—	—	31	1,702	20	1,098	123	6,753
34	82·3	—	—	28	2,304	43	3,539	77	6,337	41	3,374	3	247	3	247	—	—	889	73,165	—	—	14	1,152	—	—	—	—	28	2,304	284	23,373
35																															
36	43·9	—	—	—	—	—	—	1	44	3	132	5	220	8	351	—	—	60	2,634	—	—	10	439	10	439	20	878	90	3,951	289	12,687

Table III. Numbers /m.³ of less common zooplankton, Cruises VI-X, Sir Lancelot, 194

CRUISE VI

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Acartia clausi														6						
Centropages hamatus																				
Isias clavipes																				
Longipedia			1																	
Metridia lucens			0	0																
Oithona similis		1	3	12			8	14	39		58	41	17	6				15	42	23
Podon leuckarti					3															

Species \ Station	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Acartia clausi														11						
Centropages hamatus																		11		
Isias clavipes				4									4							
Longipedia																				
Metridia lucens																				
Oithona similis	23	17	23	30	46	46	54	85	60	16	8	23	17	15			5		21	24
Podon leuckarti																				

CRUISE VII

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Acartia clausi	8		15	19	15	9				8			11	9		
Centropages hamatus				9	7											
Isias clavipes																
Oithona similis	8	10	22	37	52	104		114	64	67	19	54	34	9	16	

Species \ Station	18	19	20	21	22	23	24	25	26	27	28	29			32	
Acartia clausi																
Centropages hamatus																
Isias clavipes								7								
Oithona similis				13		19		46	26	24	17	29				

CRUISE VIII

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
Acartia species																		
Acartia clausi																		
Anomalocera patersoni																		
Centropages hamatus					15												8	
Evadne nordmanni																		
Oithona spp.	97	29	79	215	292	129	38	25	111	123	260	70	26	89	12	56	180	1
Podon leuckarti																		

Species \ Station	21	22	23	24	25	26	27	28	29	30	31	32	33	34 FL 1	35 FL 2	36 FL 3	37 FL 4	38 FL 5	39 FL 6
ecies			26	18															
ausi					13	7	10					36	16						
era patersoni ..															2				2
es hamatus ..												7							
rdmanni																	48	25	333
pp.	39	8	146	123	47	28	91	17	48	212	93	157	79	26	51	278	762	222	222
ckarti																	127	148	178

CRUISE IX

Species \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Acartia clausi															
Anomalocera patersoni ..															
Centropages hamatus ..	11														
Oithona	464	318	46		33	26		22	26	39	8	110	72	19	55

Species \ Station	16	17	18	19	20	21		23	24	25	26	27	28	29
Acartia clausi								7			37	91	25	
Anomalocera patersoni ..				2										
Centropages hamatus ..	8	19		9	10			21	62	117	47	52	13	
Oithona	15	38	35	54	73	67		49	115	25	65	130	38	34

CRUISE X

s \ Station	1	2	3	4	5	6 FL 2	7 FL 3	8 FL 4	9 FL 5	10 FL 6	11	12	13	14	15	16	17	18
clausi		175	226		11				18							9		
ages hamatus ..		146	226	40					200	42	505		38	6	19			
us anglicus				10														
la						10												
nordmanni		379	397	382	11	10	40	477	528	375	23	2063	482	63	74	108	72	138
era wollastoni ..		1	3															
lucens																2	2	
similis	240	962	589	121	126	99	50	442	346	208	427	493	697	215	148	152	61	158
uckarti	69	699	100	70				124	73	42	16	1525	203	13			10	30

s \ Station	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34		36 FL 1
clausi	7	20								44	23	168	61	10	20	7		
ages hamatus ..									8		23		75	118	31	14		10
us anglicus																		
a			7															
nordmanni	102	101	7	5		43	32	20	74	118	215	71	75	29	72	7		
era wollastoni ..																		
lucens			1		15	2	2		7		2		14					
similis	95	281	43	33	248	43	441	154	66	111	161	115	102	147	378	64		20
uckarti			7								8	9				14		

Table IV. Oikopleura sp., Sagitta sp., and Ctenophora as numbers beneath 1m.², Cruises VII-IX, Sir Lancelot, 1949

CRUISE VII			CRUISE VIII			CRUISE IX			
Station	"Oikopleura"	"Sagitta"	Station	"Oikopleura"	"Sagitta"	Station	"Oikopleura"	"Sagitta"	Ctenophor.
1	69	25	1	—	—	1	—	—	—
2	35	—	2	1	3	2	11	14	—
3	31	182	3	—	3	3	—	—	—
4	74	138	4	—	5	4	—	19	—
5	5	207	5	9	60	5	103	74	—
6	—	—	6	—	—	6	305	106	—
7	—	—	7	14	63	7	—	—	—
8	—	—	8	—	—	8	—	—	—
9	—	100	9	—	28	9	35	25	—
10	—	—	10	—	—	10	169	88	—
11	—	—	11	—	—	11	—	15	—
12	—	—	12	—	—	12	—	—	—
13	—	—	13	7	45	13	1	86	—
14	—	—	14	6	102	14	67	45	—
15	—	—	15	5	13	15	—	—	—
16	—	—	16	3	123	16	148	56	—
17	—	—	17	—	51	17	125	216	—
18	—	—	18	—	—	18	242	91	—
19	—	—	19	35	70	19	467	32	—
20	—	—	20	38	152	20	—	—	—
21	7	630	21	29	93	21	122	93	—
22	—	300	22	7	124	22	—	—	—
23	—	600	23	—	—	23	69	68	—
24	960	480	24	8	89	24	102	41	—
25	1,080	2,160	25	—	—	25	26	74	—
26	3	81	26	101	49	26	3	85	—
27	—	—	27	9	57	27	—	244	7
28	—	—	28	—	—	28	—	—	—
29	—	—	29	—	—	29	—	—	—
30	—	—	30	15	92				
31	—	—	31	10	99				
32	—	—	32	—	—				
33	—	—	33	5	72				
34	3	53							
35	—	—							
36	—	—							
37	—	68							

CRUISE VI

Depth (metres) \ Station	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
0	8	11	15	2	0	8	22	13	10	15	12	6	7	2	4	6	14	10
10	11	11	0	1	5	6	18	11	14	17	10	11	6	1	3	7	21	18
20	9	14	12	0·5	0	5	11	12	11	14	17	12	10	5	3	10	0	20
30	16		5					15	13	15	10	10	9	6		9	20	24
Bottom							12	10	0	16	14	9	9	6	11	15	22	15
Mean " Surface " .. (0, 10, 20, 30) ..	11·00	12·00	8·00	1·17	1·67	6·33	17·00	12·75	12·00	15·25	12·25	9·75	8·00	3·50	3·33	8·00	13·75	18·00

CRUISE VI—continued

Depth (metres) \ Station	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
0	12	10	11	11	6	8	6	11	6	11	9	9	6	6	4	6	10	12
10	13	9	6	6	6	6	7	7	14	10	8	16	7	5	13	7	10	10
20	12	11	11	9	6	9	9	5	11	12	12	10	9	8	12	7	19	14
30	14	0	13	6	8	8	13	6	12	13	12	12	12	8	22	8	16	11
Bottom	23	10	13	11	12	10	9	7	12	12	10	11	10	7	11	18	20	9
Mean " Surface " (0, 10, 20, 30) ..	12·75	7·50	10·25	8·00	6·50	7·75	8·75	7·25	10·75	11·50	10·25	11·75	8·50	6·75	12·75	7·00	13·75	11·75

Mean Surface: 9·76 Mean: 10·13

CRUISE VII

Depth (metres) \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
0	14	6	6	11	11	7	7	7	1	2	7	7	4	12	11	11	15	0
10	15	9	16	8	12·5	10		8	1	9	8	8	8	9	11	7	8	0
20	11	8	9	8	10	8		8	1	4	9	3	3	5	8	7	8	0
30	10	7	17	9	7	14		11	7	11	9	4	7	7		12	11	0
Bottom	9	11	12·5	8	9	8	6	11	5	9	17	11	13	16	12·5	12·5	14	0
Mean " Surface " (0, 10, 20, 30) ..	12·50	7·50	12·00	9·00	10·12	9·75	7·00	8·50	2·50	6·50	8·25	5·50	5·50	8·25	10·00	9·25	10·50	0·00

CRUISE VII—continued

Depth (metres) \ Station	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
0	0	5		4	8	4	3		7	6	2	7	8	15	12		3	6
10	0			2	0	1			8	6	14	12	9	12	8		8	7
20	0			7	0	7			11	12	12	12	9	8	7	1	4	6
30	0			2	0	7		18	11			9	7	8	11			8
Bottom	0	2		0	18	11	14	12					7	11		3	3	
Mean "Surface" .. (0, 10, 20, 30) ..	0·00	5·00		3·75	2·00	4·75	3·00	18·00	9·25	8·00	9·33	10·00	8·25	10·75	9·50	1·00	5·00	6·75

Mean Surface: 7·38 Mean: 7·73

CRUISE VIII

Depth (metres) \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
0	6	10	8	8	12	4	1	0	3	5	7	12	8	5	1	1	4
10	10	11	7	8	13	6	5	0	0	6	8	8	10	12	1	1	4
20	10	7	10	7	12	2	4	4	0	4	5	8	11	9	4	5	6
30	9	8	5	12	2	6	3	0	2	1	5	6	11	8	6	7	10
Bottom				11	3	5	1	0	9	2	12	10	10	6	10	7	9
Mean "Surface" .. (0, 10, 20, 30) ..	8·75	9·00	7·50	8·75	9·75	4·50	3·25	1·00	1·25	4·00	6·25	8·50	10·00	8·50	3·00	3·50	6·00

Mean Surface: 6·09 Mean: 6·21

CRUISE IX

Depth (metres) \ Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
0	3·6	6·0	21·5	12·5	3·7	13·6	7·5	6·0	5·0	8·0	3·6	7·2	22·0	2·5	3·6
10	0·0	7·0		9·5	3·8	8·5	6·5	9·0	11·0	10·6	6·0	7·0	10·0	9·5	5·4
20	0·5	15·8	22·0	10·0	2·0	9·8	6·8	12·0	23·0	13·6	4·0	4·0	10·0	8·0	8·5
30	1·5	11·0	10·0	9·5	2·0	15·5	4·5	9·0	3·0	5·8	3·6		15·0	9·5	11·0
Bottom	3·6	11·2	7·5	7·4	1·5	21·8	15·8	12·5	15·0	15·5	9·0	14·0	17·5	14·6	14·8
Mean "Surface" (0, 10, 20, 30) ..	1·40	9·95	17·83	10·38	2·88	11·85	6·32	9·00	10·50	9·50	4·30	6·07	14·25	7·38	7·12

CRUISE IX—*continued*

Depth (metres) \ Station	16	17	18	19	20	21	22	23	24	25	26	27	28	29
0	6·0	5·0	4·0	3·0	16·8	12·0		5·0	0·8	1·0	2·5	5·0	3·2	0·0
10	4·5	7·5	4·2	7·0	15·0	8·0		0·0		1·8	8·6	3·6	1·5	2·0
20		4·8	6·5	4·5	11·5	5·0		3·4	0·0	4·0	4·5	3·0		1·0
30	12·0	9·0	7·0	7·0	11·0	13·5		0·0	12·0	9·0	6·5	6·0	14·6	10·0
Bottom		9·0	14·0	12·0	17·5	15·0		10·0	15·0	11·0	15·4	6·7	11·0	7·0
Mean "Surface" (0, 10, 20, 30) ..	7·50	6·58	5·42	5·38	13·58	9·62		2·10	4·27	3·95	5·52	4·40	6·43	3·25

Mean Surface: 7·33 Mean: 8·28

Dates of the SIR LANCELOT 1949 cruises referred to in this publication:

CRUISE VI	April 10–18
CRUISE VII	April 23–30
CRUISE VIII	May 10–16
CRUISE IX	May 24–27
CRUISE X	June 8–14

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